THE GROWTH AND DEVELOPMENT OF *ANTHURIUM ANDRAEANUM*. LIND FLOWER BEFORE AND AFTER EMERGENCE

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MASTER OF SCIENCE

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ABSTRACT

The red commercial cultivar, *Anthurium andraeanum* 'Kaumana' flower growth and development before and after emergence in the generative phase was studied. Before emergence, the anthurium flower was seated at its subtending leaf petiole base and enclosed by two tightly rolled stipules. The smallest flower bud that could be seen was about 0.3 cm long with its subtending leaf still in the leaf sheath and was about 4.5 cm when it was ready to emerge from the petiole base. This period took about 80 days. A slow growth period, when the flower bud was 0.8 to 1.0 cm long, occurred just after the subtending leaf emergence and when the subtending leaf petiole was in its rapid elongation period. Flower bud growth resumed after the subtending leaf blade unfurled and became autotrophic. Spathe color development started about 28 days before emergence when the flower bud was about 50% of the emergence bud length. The two lobes were the last to develop. They were visible when spathe color started developing. At flower emergence the spathe was 80% red, with the lobe still white. Flower stalk elongation started 28 days before flower emergence.

Flower stalk growth was sigmoid-shaped with the maximum growth rate 21 days after emergence. Flower spathe growth had a double sigmoid growth curve. The spathe was tightly furled for about 35 days after emergence. The spathe unfurled after the flower stalk had reached its maximum growth rate. Spadix growth study was possible only after the spathe was unfurled and matured from the base

to the tip. Spathe lobe was not red until 7 to 10 days after flower emergence.

Young subtending leaf blade (7 to 14 days after leaf emergence) had a negative net photosynthetic rate. Removal of this leaf blade promoted earlier flower emergence by 18 days. Soft green leaf (25 to 30 days after emergence) had a slightly positive net photosynthetic rate, and the removal of this leaf resulted in 11 days earlier flower emergence. A mature subtending leaf had the highest net photosynthetic rate, and its removal had little effect on flower emergence.

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INTRODUCTION

The anthurium (*Anthurium andraeanum* Lind.) is an ornamental flower grown in tropical or near-tropical climates. In the United States anthuriums are grown chiefly in Hawaii and southern California and nearly all are sold as cut flowers (Walker and Smith, 1978). The flower consists of a modified leaf (spathe) which subtends a cylindrical inflorescence called a spadix (Marutani, 1984). The spadix is covered with hundreds of tiny true flowers (Higaki and Watson, 1967). The heart-shaped spathe is approximately 7 cm x 10 cm (Walker and Smith, 1978). The major commercial cultivars are red Ozaki, Kozohara and Kaumana, and orange Nitta. Characterized by its showy spathe, anthurium is the most important flower crop in Hawaii (Hawaii Agricultural Statistics, 1987).

In late 1981, a flower development disorder referred to as "bleach" was first described in a commercial anthurium field (Nishijima, 1981). Nishijima (1981) described the problem: " usually first appears as small purple spots with a small necrotic center on the back side of the spathe. Subsequent symptoms in more or less chronologic order of appearance include burning of young leaves, lesions or spots on leaves and petioles, severe chlorosis and stunting of new leaves and bleaching of developing flowers. .....It was estimated that within a month, 30% of the anthurium acreage under saran became affected. ..... The bleaching problem is proving to have a greater economic impact than the blight." Bushe, et al. (1987) described the "bleach" problem: "In mild cases impaired color development occurs

in the lobe area of the spathe, and in severe cases the entire flower including the spadix may show signs of insufficient color development, stunting, distortion and necrosis". No clear correlation was found between the occurrence of the disorder and prior environmental conditions or field management (Leonhardt, 1989, personal communication).

The "bleach" symptoms suggest a disruption of the normal flower development, and seem to be a problem associated with the development of anthocyanins before the flower emerges from the subtending leaf petiole base. The period before flower emergence has not been studied in detail. In order to study the "bleach" problem, it is very important to obtain information about the sequence and timing of spathe, spadix, and lobe development before and after flower emergence to determine when anthocyanin synthesis starts. The information from such a study would not only help in solving the "bleach problem" but also other problems which may occur in flower development.

The major problem in determining flower bud development before emergence is that it is destructive. One approach would, therefore, be to use a statistical procedure of sampling from a population of uniform plants growing under the same conditions and dissecting the plants at a series of times. Another approach could be to find a developmental index. If this developmental index has a certain relationship to the flower bud growth before emergence and this relationship would not change under various conditions (weather, water, soil, etc.), then the flower bud

growth before emergence can be predicted without damaging the plants.

The present study was initiated to determine the time and sequence of flower stalk, flower spathe, spadix and lobe growth and development before and after flower emergence, to determine the crucial time of flower spathe anthocyanin synthesis and to find an appropriate development index for anthurium flower bud growth and development before emergence, with an especially focus on *A. andraeanum* 'Kaumana'.

LITERATURE REVIEW

Botany and Biochemistry

Taxonomy

The anthurium belongs to the family *Araceae* which includes more than 100 genera and about 1,500 species, mainly from the tropics. The neotropical genus *Anthurium* is the largest and possibly the most complex genus of the *Araceae*. The genus is taxonomically difficult due to the large number of species in the genus and considerable morphological plasticity in most structures. There are an estimated 600 to 800 species in this genus (Croat and Bunting, 1979).

Anthurium andraeanum, a native of Central America, was first introduced to Hawaii from London in 1899 by S. M. Damon (Hieronymus, 1949; Higaki and Watson, 1967). Since that time, many other species have been introduced, and hundreds of hybrids have been developed (Hieronymus, 1949).

Morphology

Anthurium andraeanum Lind. is a low-growing perennial, herbaceous monocotyledon plant with cordate leaves and flower bracts. The leaf is simple, green, cordate with entire margins, and at maturity is usually 20 x 30 cm long. The leaf blade is attached to a cylindrical petiole that basally forms a fused sheath around the stem. The petiole is smooth and usually 25 to 35 cm long. Stipules are

borne at the sheath and stem junction on mature leaves, covering the flower bud in its early stages.

The stem has nodes approximately 1 cm to 15 cm apart, depending on the cultivar and the environment. Increased shade promotes longer internodes, whereas high light produces shorter internodes regardless of cultivar. The leaves have a spiral arrangement on the stem. A vegetative, adventitious, lateral bud is formed at alternate nodes, opposite each leaf junction. The vegetative buds are helically arranged and opposite the leaves. The roots are adventitious and originate from the stem nodes.

Flower buds are borne in each leaf axil. A mature inflorescence has a conspicuous bract (spathe) joined to the base of a cylindrical spike (spadix) and attached to a long peduncle. The spathe is usually 12 x 14 cm, has a uniseriate upper and lower epidermis with one or two layers of hypodermal cells and 10 to 12 layers of spongy parenchyma cells. Anthocyanin are localized in the hypodermal cells. In various colors, the spathe is the product for which anthurium is grown commercially.

The botanical flowers are minute and perfect, and there are about 300 flowers arranged helically on the spadix (Higaki, et al. 1984). The individual flowers are made up four fleshy sepals situated conjugately (the perianth), four stamens, and one upper and fleshy pistil. The pistil grows earlier than the stamens. The stamens develop 3-4 weeks after full growth of the pistil. The period can be

shortened, however, depending on the temperature and the humidity of the environment (Szendel and Weryszko, 1973). The proximal flowers mature first with development progressing toward the apex. The flowers are protogynous, and the stigma is receptive before the pollen is shed (Higaki, et al. 1984). The proximal flower matures first with development progressing towards the apex. The time lapse between stigma receptivity and dehiscence is about a week. The mature peduncle is smooth, cylindrical, and approximately 40 to 60 cm in length and 0.5 cm in diameter.

Fruits are small, globose, yellow berries closely arranged on the spadix. There are two seeds per berry. The seeds germinate immediately after sowing and the first flower is produced about 18 months after germination (Higaki, et al., 1984).

When propagated by seed, *Anthurium* goes through a juvenile phase in which a vegetative axillary lateral bud is formed at alternate nodes, opposite each leaf junction. As the plant matures, a generative phase follows. The difference between the two phases is in the axillary buds. In the juvenile stage, leaves have short sheath with a vegetative bud in the axil, whereas in the generative stage an inflorescence bud is seated in the axil of the leaves. Instead of a leaf sheath, the covering of the axil and upper part of the petiole base protecting the inflorescence bud is composed of stipules (Christensen, 1971; Higaki, et al., 1984).

The vegetative apical meristem is offset from the center of the shoot (Higaki, *et. al*, 1984). At the meristematic apex are two layers of tunica cells which divide

perpendicularly to the surface of the meristem, and beneath the tunica is the corpus where cell division occurs in several planes. The corpus adds bulk to the apical portion of the shoot by increasing in volume, whereas the tunica maintains its continuity over the enlarging body by surface growth (Higaki, *et al*, 1984).

Flowers are produced throughout the year after the juvenile phase has been passed (Kamemoto and Nakasone, 1963). The anthurium plant produces flowers in a very definite cycle of flower-leaf-flower (Walker and Smith, 1978). In the case of the cultivars Kaumana and Nitta, the flower emerges about a month after the subtending leaf appears and precedes the new leaf by a few weeks. This sequence of leaf, flower, and new leaf is maintained throughout the plant's life. The intervals between leaf emergences varies with season. More flowers appear during the summer months when conditions are favorable for growth, whereas less flowers are produced during winter when temperatures are lower and daylength is shorter (Kamemoto and Nakasone, 1963).

Watson and Shirakawa (1966) related flower development of anthurium to the inflorescence shelf life. They concluded that a more mature inflorescence had a longer shelf life. But commercial flower harvest takes place when approximately three quarters of the stigmas along the spadix have become receptive (Criley, 1985). The flower is long-lasting, often having a shelf life of 4 weeks (Kamemoto and Nakasone, 1963; Paull, *et al.* 1985). The size, shape and color of the showy spathe determines the commercial value of the flower (Paull, 1985).

Cytology

The most common somatic chromosome number found was 30, but counts range from 2n = 20 to 90 (Sheffer and Kamemoto, 1976). Chromosome numbers for anthurium were reported as 2n = 30 (Gaiser, 1927; Sheffer and Kamemoto , 1976; Simmonds, 1954), and 2n = 32 (Tsuchiya and Takada, 1962). The chromosome number is 2n = 30 for *Anthurium andraeanum* Linden 'Kaumana', which originated in Kaumana, and 2n = 20 + 2B for 'Uniwai' (Kaneko and Kamemoto, 1978), a white-spathe cultivar released by the University of Hawaii in 1962 (Kamemoto and Nakasone, 1963).

Pigmentation

Iwata, et al., (1979) identified the anthocyanins in the spathes of anthurium as cyanidin 3-rhamnosylglucoside and pelargonidin 3-rhamnosylglucoside. Both pigments are present in the red cultivars, including Ozaki, Kaumana, Kozohara, Kansako No.1, and Nakazawa and also in the pink cultivar Marian Seafurth. The orange cultivar, Nitta and the coral colored Tateishi Coral contains only pelargoidin 3-rhamnosylglucoside. Recently, Marutani, et al., (1987) identified the two anthocyanins from *Anthurium amnicola* (Dressler), a newly discovered species from Panama, as cyanidin 3-rutinoside and peonidin 3-rutinoside. Using HPLC technique, they found that the anthocyanins in the spathe and spadix were similar, and the

cyanidin-rutinoside was the major anthocyanin with peonidin 3-rutinoside as the minor one.

Spathe color is determined by relative concentrations of the anthocyanins cyanidin 3-rhamnosylglucoside and pelargonidin 3-rhamnosylglucoside in *Anthurium andraeanum* Linden ex Andre. Pink to dark red colors are the result of a predominance of cyanidin 3-rhamnosylglucoside, whereas a predominance of pelargonidin 3-rhamnosylglucoside results in coral to orange (Iwata, et al., 1985). As the color become lighter, the concentrations of each pigment decrease (Iwata, 1980).

Because of the presence of two anthocyanins in red and pink spathes, Iwata (1980) suggested that two major genes were responsible for anthocyanin production. The gene M controlled production of cyanidin 3-rhamnosylglucoside, and the gene O controlled production of pelargonidin 3-rhamnosylglucoside (Iwata, 1980). Later, Kamemoto, et al. (1988) concluded that these two genes, M and O, are responsible for the five major colors of anthuriums (*Anthurium andraeanum* Hort.): red, orange, pink, coral, and white. The gene M controls the production of cyanidin 3-rutinoside, and the gene O is responsible for the production of pelargonidin 3-rutinoside. Red and pink result when both genes are present, and orange and coral result when only O is present. White results when either the double recessive gene, mmoo, or M combined with oo (MMoo, Mmoo) is present. Colors are also affected by the dosages of M and O. The incremental effects of M appear to be greater than O,

and the intensity of colors decreases from MMOO, MMOo, MmOO, to MmOo. Orange is mmOO, and coral is mmOo (Kamemoto, et al., 1988).

Many enzymes are involved in anthocyanin synthesis, but the specific steps in the biosynthesis are not well known (Mancinelli, 1983). Chalcone isomerase (CHI), an enzyme specific to the flavonoid (including anthocyanin) biosynthesis pathway (Hahlbrock 1981), and phenylalanine ammonia-lyase (PAL) are regarded as the rate-limiting enzymes in anthocyanin synthesis (Hahlbrock 1981; Chappell and Hahlbrock 1984). Increases in PAL activity have been associated with anthocyanin synthesis in several plant tissues (Hyodo, 1971; Creasy, 1968). Methyltransferase controls the methylation of the B-ring in flavan, the terminal reaction in anthocyanin biosynthesis (Carmel et al 1974). The capacity for the formation of anthocyanin is determined by hereditary factors (Mancinelli, 1983). Many genes control the biosynthesis of anthocyanin and flavonols (Gerats, 1982).

Studies have shown that anthocyanin synthesis in the skin of apple fruit (*Malus sylvestris* Mill. cv. Jonathan) is light-dependent (Chalmers and Faragher, 1977a) and may be regulated by the activity of PAL. Faragher and Chalmer (1977) found that the PAL activity was induced by exposure to white light. The action of light on anthocyanin production has been extensively used as a biochemical model system for the study of the mechanism of photoregulation of plant growth and development (Mancinelli, 1983). The general characteristics of the action of light on anthocyanin production are those typical of the High Irradiance Response (HIR)

of plant photomorphogenesis (Mancinelli, 1980b; Mancinelli and Rabino, 1978; Mohr, 1972; Shropshire, 1972a; Smith, 1975) which requires prolonged exposures to high fluency rates of visible and near visible radiation for its full expression. The spectral sensitivity and rate of anthocyanin production are different in different systems and influenced by physical, chemical, and biological factors (Mancinelli, 1985). Hendricks and Borthwich (1959) first suggested that phytochrome was involved in the photoregulation of the HIR and that the characteristic features of this class of photoresponses was a manifestation of the action of the pigment under conditions of continuous excitation (Mancinelli, 1983). The expression of the HIR depends upon the presence of the physiologically active and unstable form of phytochrome, Pfr, either as such or as an overcritical activated form, Pfr*, or as a bound form, Pfr-X over a prolonged period of time.

Horticulture

Propagation

Anthurium can be propagated by seeds or vegetative shoots. Seeds are hard to obtain, however, unless the grower is extremely alert and has sufficient flowers available so that pollen can be taken at any time from different plants. The reason is due to the different times of maturity of the pistil and stamens (Hieronymus, 1949). Controlled pollination is accomplished by grasping the pollen-laden spadix with the fingers and then transferring the pollen to the receptive stigmas of another

flower by rubbing the spadix with the same fingers. The yellow berries are formed 6 to 7 months after pollination and fertilization. The berries are collected, and the seeds are squeezed out of the pulp with gentle pressure. The seeds can be planted into media immediately (Higaki and Watson, 1967).

Old plants often produce small shoots that may be taken as soon as the small, fleshy, aerial roots appear (Hieronymus, 1949). One common method of increasing a particular cultivar, described by Higaki and Watson (1967), is to grow the plant until some roots have developed high on the stem near the top. The top with these roots is then removed to produce a new plant. The remaining base of the stem with its roots will then produce two or more side shoots (suckers). By repeating this procedure large numbers of plants may be propagated (Higaki and Watson, 1967).

It is advantageous to root cuttings (terminal cuttings with relatively few leaves and no roots) under intermittent mist. If plant material is very limited, additional cuttings can be prepared by sectioning the topped stem into various lengths each containing at least 1 node and 1 axillary bud (Kunisaki and Sagawa, 1971).

Plant Selection

The standards of a desirable plant, spathe, and spadix have been set by Higaki and Watson (1967). A desirable plant should grow vigorously and be a prolific producer of suckers and flowers. Short internodes are better than long ones

in order to limit the height of the plant. A desirable spathe is heart-shaped with symmetrical, overlapping or fused lobes. Good spadix should be somewhat shorter than the length of the spathe. A gentle reclining of spadix is preferred to facilitate packing for shipment (Higaki and Watson, 1967).

Environment

Growth Media

Anthuriums grow in a high organic, well-aerated medium with good water retention and good drainage. Higaki and Watson (1967) described: " A good medium needs to be able to anchor the roots and stem so that the plant will not topple over as it grows upward yet provide sufficient moisture, nutrients, and aeration to the plant. Wood shavings, sugar-cane bagasse, tree-fern chips, taro peel, macadamia nut shells, or coffee parchment will serve as a good medium to anchor the roots." Some growers also grow anthuriums between rocks or volcanic cinders to anchor the roots, and provide a mulching with bagasse to retain the moisture (Higaki and Watson, 1967).

Light

Anthurium plants do not thrive well under high light intensity, and shade must be provided for satisfactory growth and flowering (Nakasone and Kamemoto, 1962). The degree of shading varies with the cultivar, age of the plant, and climate

under which the plant is grown. The shade required usually ranges from 50 to 90 percent of full sunlight, and insufficient shading often results in damage to leaves, even death of the plant (Higaki and Watson, 1967). In general, there is an increase in stem length and spathe size with increasing shade, whereas flower production increases with light intensity increases (Nakasone and Kamemoto, 1962). Saran cloth houses, lath houses, plantings of tree fern (*Cibotium chamissoi*) and citrus or lychee trees can provide shade for anthurium growth (Higaki and Watson, 1967).

Temperature

Anthuriums thrive when the night temperature is not lower than 18 ^{o}C and the day temperature is about 27^{o}C (Higaki and Watson, 1967). Temperature affects flower development inside the petiole base and elongation of the peduncle axis, but this factor has not been studied in anthurium (Criley, 1985). Flower initiation and development proceed at 18^{o}C and above with an optimum of 20^{o}C and higher (Higaki and Watson, 1973). Leaf-cooling has been reported to improve flower production of *A. andraeanum* under conditions of high light intensity (Leffring, 1975). A Netherlands study suggests that a concentration of flowering of *A. scherzerianum* clones in late springtime may be related to cool winter greenhouse temperatures, and flower development is promoted by lowering the night temperature to a constant 12 ^{o} or 15 ^{o}C for 6 weeks before returning the plants to

21°C. The optimum temperature for both growth and flowering is 19°C (Szendel and Weryszko, 1973).

Nutrition

Nutrition affects flower production and quality. Increasing nitrogen fertilization (126 mg N per pot per week up to 396 mg N per pot per week) decreased flower production and quality, and 187 mg K per pot per week was the optimum K level for *A. andraeanum* (Bik, 1976). Calcium deficiency can lead to a color breakdown disorder in the spathe (which is different from bleach problem) and the critical calcium level was determined as 0.14 to 0.16 in the spathe (Higaki, 1977, Higaki *et al.*, 1980).

Growth Regulators

Cytokinins have been reported to modify anthurium flower yield by increasing lateral branches (Higaki and Rasmussen, 1979). Ethylene appears to inhibit anthocyanin production (Buhler, et al., 1978, Craker et al., 1971, Kang and Burg, 1973), and the depression of anthocyanin biosynthesis in various plant systems has also been reported for IAA or NAA (Arnold and Albert, 1964, Vince, 1968), for GA_3 (Arnold and Albert, 1964, Hinderer, et al., 1984, Vince, 1968), and for Zeatin (Tong, et al., 1983). Since auxins, cytokinins and gibberellic acid promote ethylene production (Abeles, 1973), the possibility exists that the inhibiting effect of the

above-mentioned growth regulators on anthocyanin biosynthesis is mediated by ethylene (Rengel and Kordan, 1987).

Postharvest Life

Anthurium flower is long-lasting, often having a shelf life of 4 weeks (Kamemoto and Nakasone, 1963; Paull, et al., 1985). The senescence of flowers is not due to a shortage of carbohydrates, but probably due to water stress (Paull, et al., 1985). Silver nitrate pulsing reduced the water uptake rate decline and helped to maintain an increased rate 10 days after harvest. Water loss can be reduced by waxing the whole flower with carnauba and other commercial fruit waxes. Waxing with FMC-819 (a commercial wax) can double postharvest life (Paull and Goo, 1985).

MATERIALS AND METHODS

Plants Growing Conditions

One hundred and sixty young terminal cuttings (2-leaved, 30 to 40 cm long) from 3 to 4 year-old plants of *Anthurium andraeanum* cv. 'Kaumana' were obtained from a commercial grower on the island of Hawaii in June, 1987. They were harvested in the morning and received at Honolulu in the afternoon. They were potted into wood shaving in 16 x 18 cm (height x radius) pots in a glasshouse in which a Saran cloth house was installed to provided a shade of 73% of full sunlight. The average photon flux density was 55 uE m^{-2} sec^{-1}, and daytime average temperatures were 20 ^{o} to 22 ^{o}C during January to April. Night temperatures were 16 ^{o} to 18 ^{o}C during this period. From April to June, daytime temperatures were 24 ^{o}C to 28 ^{o}C, and night temperatures were 20 ^{o} to 22 ^{o}C. The average photon flux density was 70 uE m^{-2} sec^{-1} during this period. Irrigation was supplied automatically from overhead sprinklers for 5 minutes twice a day, and relative humidity was kept 80% $\pm$ 20% for the whole growth study period. Osmocote (18: 6: 12) fertilizer was supplied (15 gm pot^{-1}) once a month. Micronutrients as Foliar-60 were also applied to the medium, about 0.75 gm pot^{-1}, once every three weeks. Healthy plants with an average height (from pot level to top of the plant) of 42 cm and with about 3-4 fully expanded leaves (25 cm in length and 13 cm in width) were chosen at random for this study.

Twenty plants of 'Marian Seafurth' were also bought at the same time with 'Kaumana' and grown under the same conditions as 'Kaumana'. The purpose of using 'Marian Seafurth' originally was to compare the flower growth and development before and after emergence with 'Kaumana'. Only part of the growth after emergence, however, was studied due to not enough plant materials.

Plant Growth and Development Evaluation

The experiment started in January 1988. At that time, most 'Kaumana' plants had already flowered, and new flowers were emerging. The plants bearing the second flower were tagged, and the length of the flower stalk (length from the flower stalk base to the junction of the stalk and flower spathe), length of spathe (junction to spathe tip) and of spadix were measured. Growth rate was estimated as change in length or width divided by change in days. Spadix length was measured after spathe unfurling, and the maturity was determined as the percentage of mature minute flowers on the spadix. Immature minute flowers were yellow on the spadix, whereas mature minute flowers were white. Flower cycle was determined as the length of time between the emergence of one flower and the emergence of the next flower in the flower-leaf-flower cycle of an individual plant. Same methods were applied to 'Marian Seafurth'.

Petiole length (length from the base of the petiole to the joint of its leaf), and leaf blade length (leaf lobe to leaf tip) were measured when the leaf had

emerged from the leaf sheath. Leaf blade width (widest part of the leaf) was also measured when leaf blade was unfurled. Growth rate was estimated as previously described. The color and the texture of the leaf blade were recorded. When determing leaf blade color, a *R.H.S. Colour Chart* (Royal Horticultural Society, 1966) was used. The leaf blade colors were matched as closely as possible with the *Colour Chart*, but in many instances it was not possible to obtain exact matching colors. The texture of the leaf blade was determined by hand as soft, hard, and very hard. The rate of CO_2 fixation and stomata aperture of the leaves at day 14, 28 and 42 after leaf emergence were determined by a LI-1600 Portable Photosynthesis System (Li Cor Inc., Nebraska) under standard conditions (in the laboratory with a light intensity of 55 uE m^{-2} s^{-1}, room temperature of 22 ^{o}C) and in greenhouse (under 73% shade) conditions. The means of the net photosynthesis rate and the standard deviations were calculated by the computer system of the LI-1600 automatically.

Flower Bud Growth and Development Evaluation

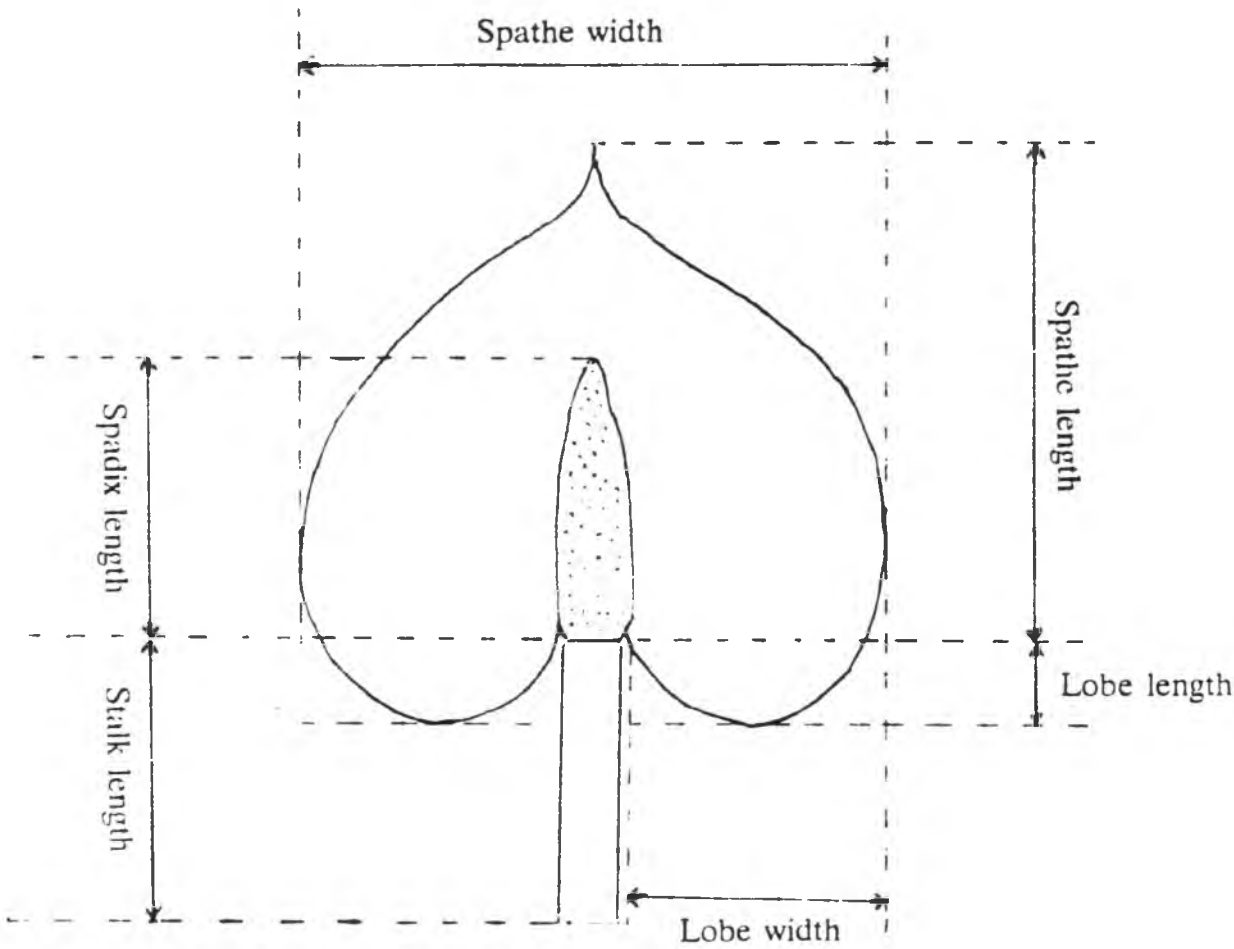
Each new leaf has a flower bud enclosed by the petiole base in the generative phase. Eight 'Kaumana' subtending leaves, each leaf on each plant, were dissected at one week interval after subtending leaf emergence, and the flower bud size was measured. The bud length (stem base to flower tip), stem length (from the base of stem to the junction of spathe), spadix length (bottom to the tip of the

spadix), spathe length (junction of the spathe with stem to the tip of the spathe) and width (widest part of the spathe, usually across the junction of stem, spathe and spadix) were measured. The length and width of lobe, as illustrated in Figure 1, was also determined after they reached 1 mm. The spathe and lobe widths could only be measured after unfurling of the spathe following killing with hot water (75 ^{o}C). The flower bud age was calculated as days after subtending leaf emergence and recalculated as days before flower emergence. The growth was determined as increase in length or width with the age. Growth rate was estimated as previously described. Color development of the bud was determined as the visible red color shown on the spathe.

Microscopic Study

'Kaumana' flower buds were placed in a small test tube containing 5 ml acetocarmine (Jensen, 1962), and heated in a water bath at 60 ^{o}C for 15 to 20 minute minutes, depending upon the hardness of the tissue. The flower bud (or sliced flower bud) was placed on a clean slide in a drop of acetocarmine and teased apart with a pair of iron needles, then covered with a cover slip. The preparation was heated gently with an alcohol lamp. A little pressure was applied to the preparation to flatten the tissue. The edges of the cover slip were sealed with wax. The preparation was examed under the light microscope.

Figure 1. *Anthurium andraeanum* flower parameters.


Spathe width
Spathe length
Spadix length
Lobe length
Stalk length
Lobe width

Subtending Leaf Removal

Subtending leaf blades from six 'Kaumana' plants, one leaf on each plant, were removed at day 7 to 14, 25 to 30, and 45 to 50 after leaf emergence. The subtending leaf blades were cut with a razor blade or removed by hand at the junction of petiole and leaf blade. The day of flower emergence from the petiole base was recorded. When the flower emerged from the control plants (plants without subtending leaf removal), the length of each part of the inflorescence from all the plants was measured, and the means and standard deviations were determined.

Cultivar Difference

The flower cycle (time from one flower emergence to the next flower emergence) and the time between subtending leaf emergence to flower emergence were compared between 'Kaumana' and 'Marian Seafurth'. Ten plants were used for each cultivar.

RESULTS

Flower And Leaf Growth After Emergence

Flower Growth After Emergence

Flower emergence was defined as the time when the flower stem emerged through the two stipules of the subtending leaf. The emergence of the flower from the petiole base was regarded as day 0. The average length (from the flower stem base to the spathe tip) of a flower just emerging from the subtending leaf petiole base was 4.5 $\pm$0.5 cm. At this time, 90% of the spathe length was red with only the lobes being white. The growth curve for the flower stem was sigmoid (Figure 2-A.). Initially, flower stem growth was slow, with a growth rate of 0.5 cm day^{-1} (Figure 2-B). Seven days later, flower stem growth had increased to 1.4 cm day^{-1}. The flower stem continued to elongate rapidly, and by day 21 it reached its maximum growth rate of 2.2 cm day^{-1}. Then, the growth rate gradually declined as the flower stem approaching its full length. Forty two to fifty days after emergence, the flower stem completely stopped elongation (Figure 2-A).

The growth curve of the spathe after flower emergence was a double sigmoid (Figure 3-A). At first, the growth rate of spathe was rapid (Figure 3-B), with a maximum growth rate of 0.17 cm day^{-1}. Fourteen days after emergence, the growth rate declined. By day 21, the spathe had almost stopped growing with a growth rate of only 0.07 cm day^{-1}. The slow growth rate lasted for about seven days and was

followed by a second peak of growth of 0.14 cm day^{-1} at day 35 and continued to day 42. This was followed by a second decline in growth rate. This decline continued to day 63 when the spathe reached to its full length.

The unfurling of the spathe occurred 35 days after flower emergence (Figure 3-A). At this stage, the spadix appeared in the middle of the spathe and became measurable. The growth of the spadix (Figure 4-A) was very fast, and the maximum growth rate (0.086 cm day^{-1}) was obtained at day 49 (Figure 4-B) after flower emergence. The growth rate declined rapidly to zero after this peak and stopped at day 77. During the period of spadix elongation, the maturity of the minute flowers on the spadix also changed. At day 35, 0 to 20% of the minute flowers on the spadix were mature and 14 days later, 50% were mature (Figure 4-A). The spadix matured an additional 20% of the flowers in the following 14 days and reached its full maturity at day 77 from flower emergence. The proximal flower matured first with development progressing towards the apex.

The growth of the two lobes after flower emergence to day 42 was constant (Figure 5-A) with a growth rate of 0.36 mm day-1 (Figure 5-B). After day 42, their growth rate doubled until day 56, then gradually decreased to zero as they became mature.

Figure 2-A. Growth of *A. andraeanum* 'Kaumana' flower stalk after emergence from late of January to April 1988. Data are the mean values of eight to fifteen flowers from the same number of plants. Bars show the variation of the flower stalk lengths.

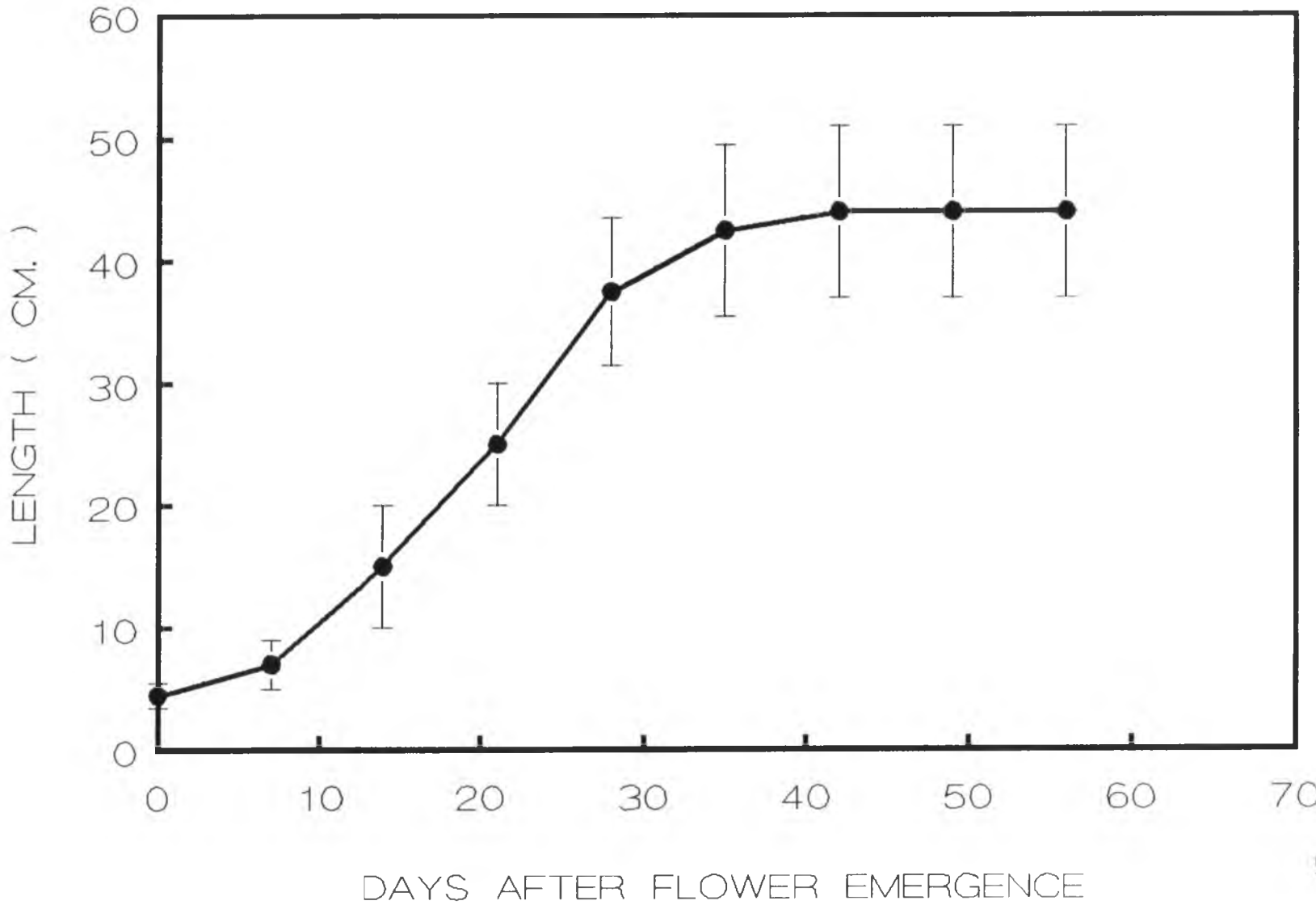

60
50
40
30
20
10
0
LENGTH (CM.)
0
10
20
30
40
50
60
70
DAYS AFTER FLOWER EMERGENCE

Figure 2-B. *A. andraeanum* 'Kaumana' flower stalk growth rate after flower emergence. The growth rate was estimated as means of flower stalk length changes divided by change in days.

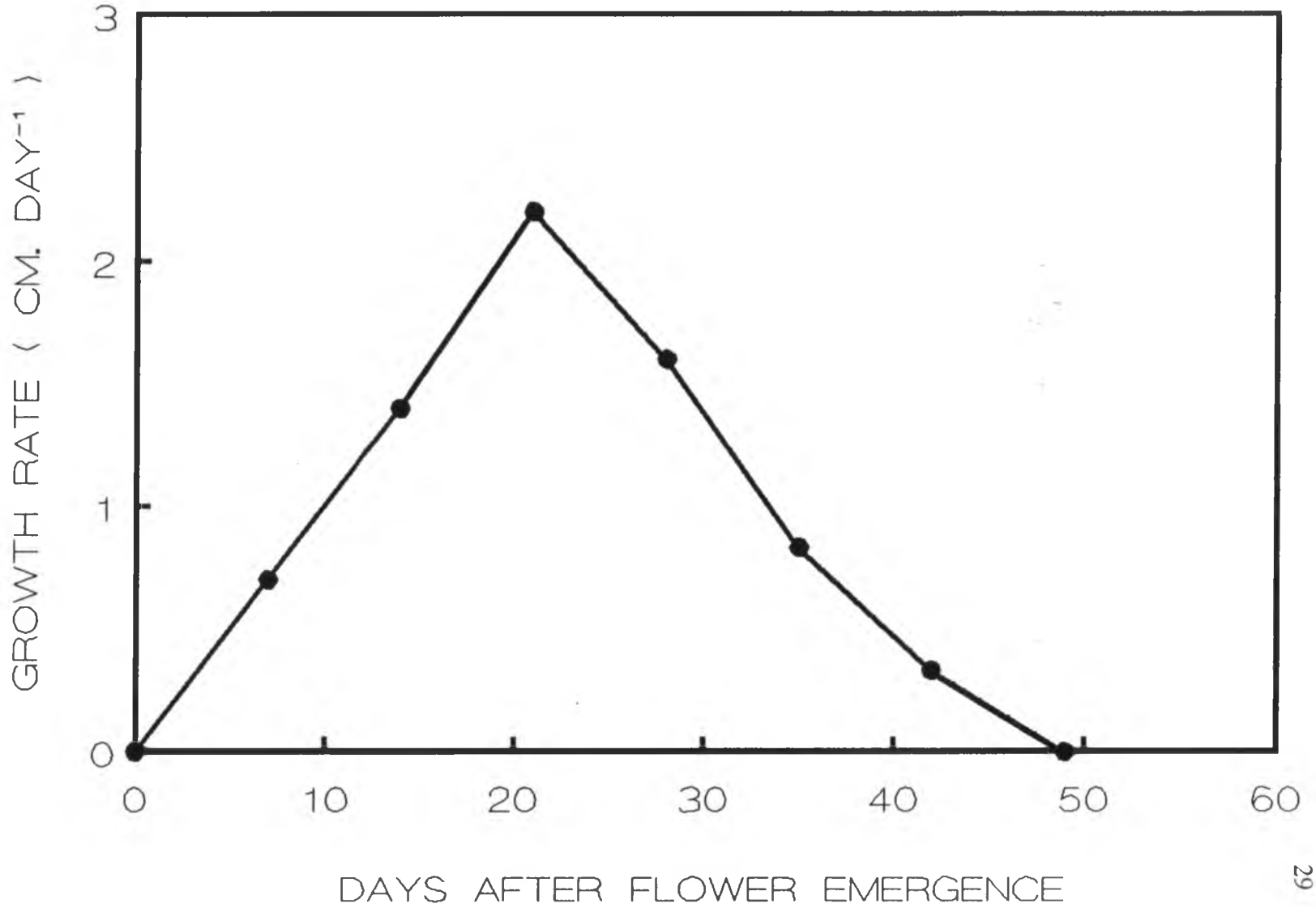

GROWTH RATE (CM. DAY-1)
3
2
1
0
0
10
20
30
40
50
60
DAYS AFTER FLOWER EMERGENCE

Figure 3-A. Growth of *A. andraeanum* 'Kaumana' flower spathe after flower emergence from late of January to April, 1988. Data are the mean values of eight to fifteen flowers from eight to fifteen plants. Bars show the variation of the spathe lengths.

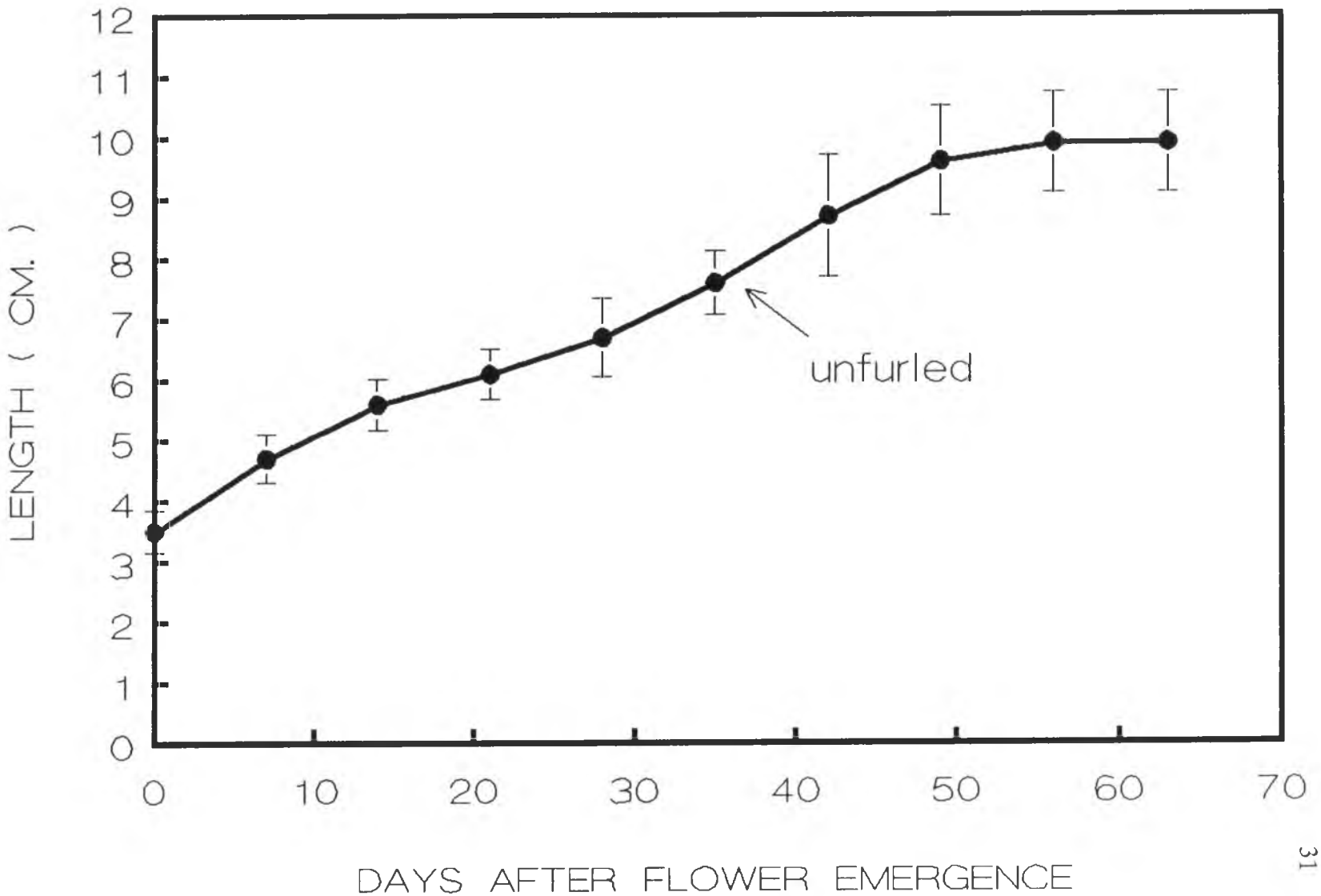

LENGTH (CM.)
0
1
2
3
4
5
6
7
8
9
10
11
12
0
10
20
30
40
50
60
70
unfurled
DAYS AFTER FLOWER EMERGENCE

Figure 3-B. *A. andraeanum* 'Kaumana' flower spathe growth rate after flower emergence. The growth rate was estimated as means of spathe length changes divided by change in days.

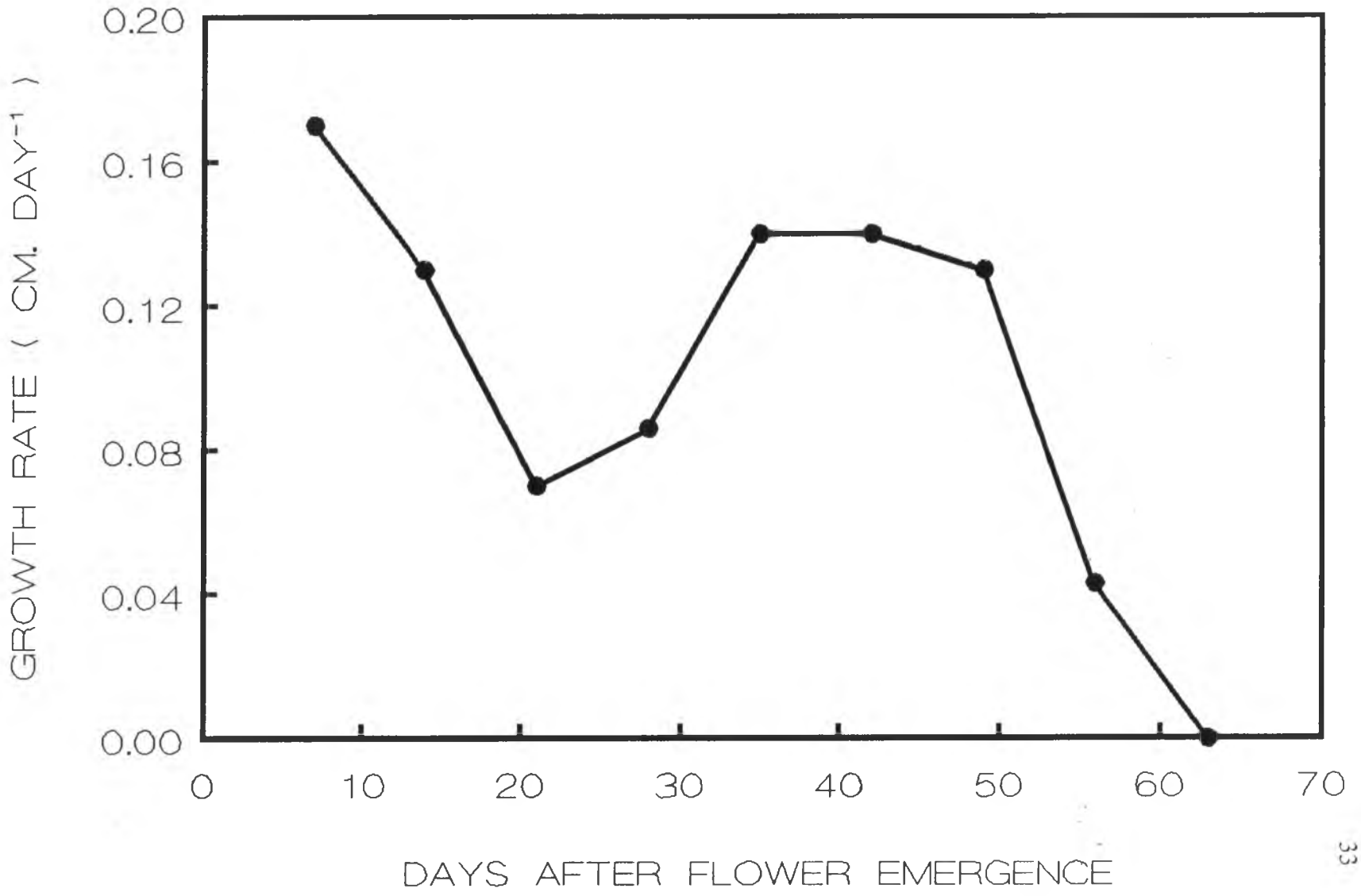

GROWTH RATE (CM. DAY^{-1})
0.20
0.16
0.12
0.08
0.04
0.00
0
10
20
30
40
50
60
70
DAYS AFTER FLOWER EMERGENCE

Figure 4-A. Growth of *A. andraeanum* 'Kaumana' flower spadix after flower emergence from late of January to April, 1988. Data are the mean values of eight to fifteen flowers from eight to fifteen plants. Bars show the variation of the spadix lengths.

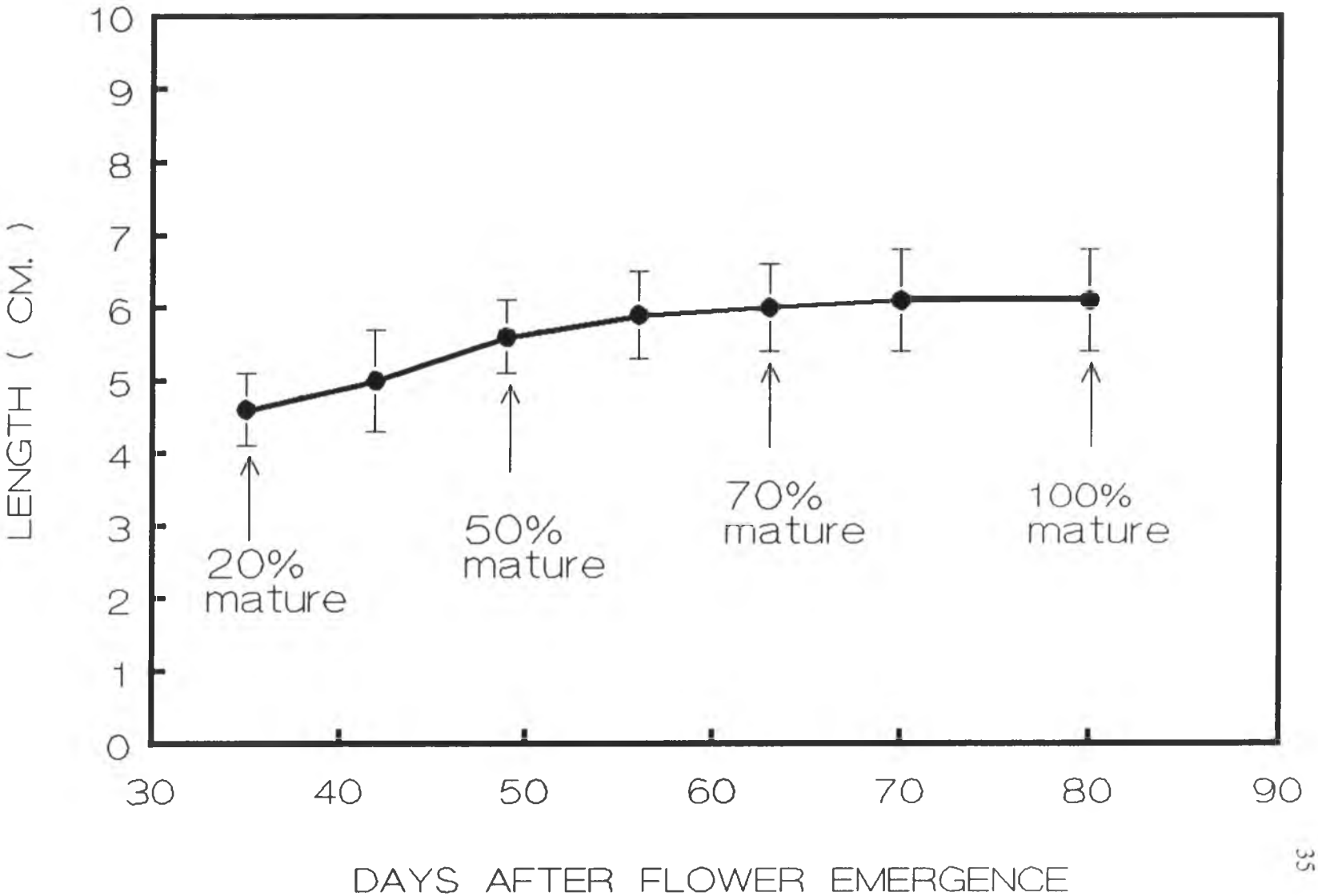

LENGTH (CM.)
10
9
8
7
6
5
4
3
2
1
0
30
40
50
60
70
80
90
20% mature
50% mature
70% mature
100% mature
DAYS AFTER FLOWER EMERGENCE

Figure 4-B. *A. andraeanum* 'Kaumana' flower spadix growth rate after flower emergence. The growth rate was estimated as means of spadix length changes divided by change in days.

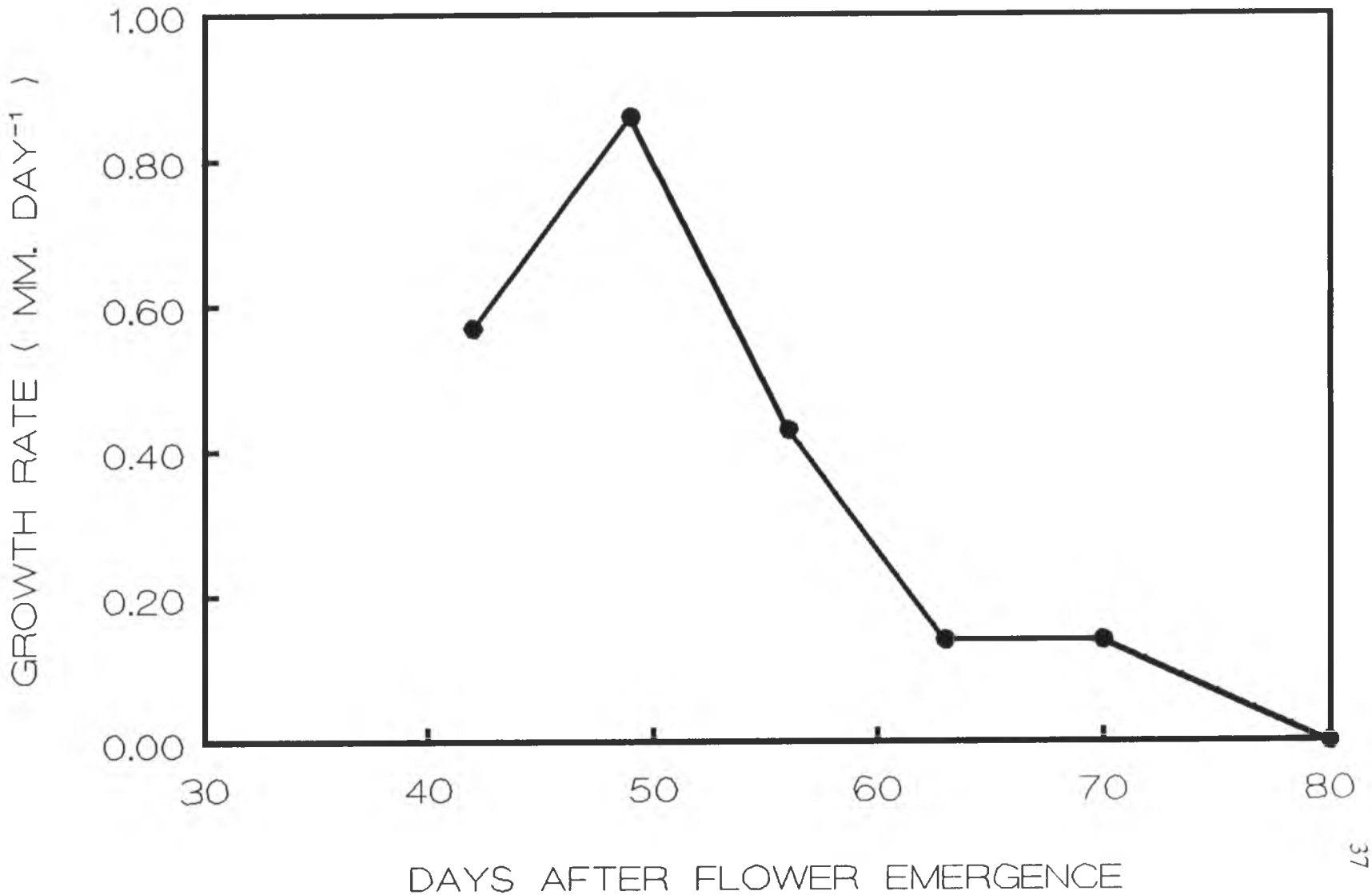

GROWTH RATE (MM. DAY^{-1})
1.00
0.80
0.60
0.40
0.20
0.00
30
40
50
60
70
80
DAYS AFTER FLOWER EMERGENCE

Figure 5-A. Growth of *A. andraeanum* 'Kaumana' flower spathe lobes after flower emergence from late of January to April, 1988. Data are the mean values of eight to fifteen flowers from eight to fifteen plants. Bars show the variation of the lobe lengths.

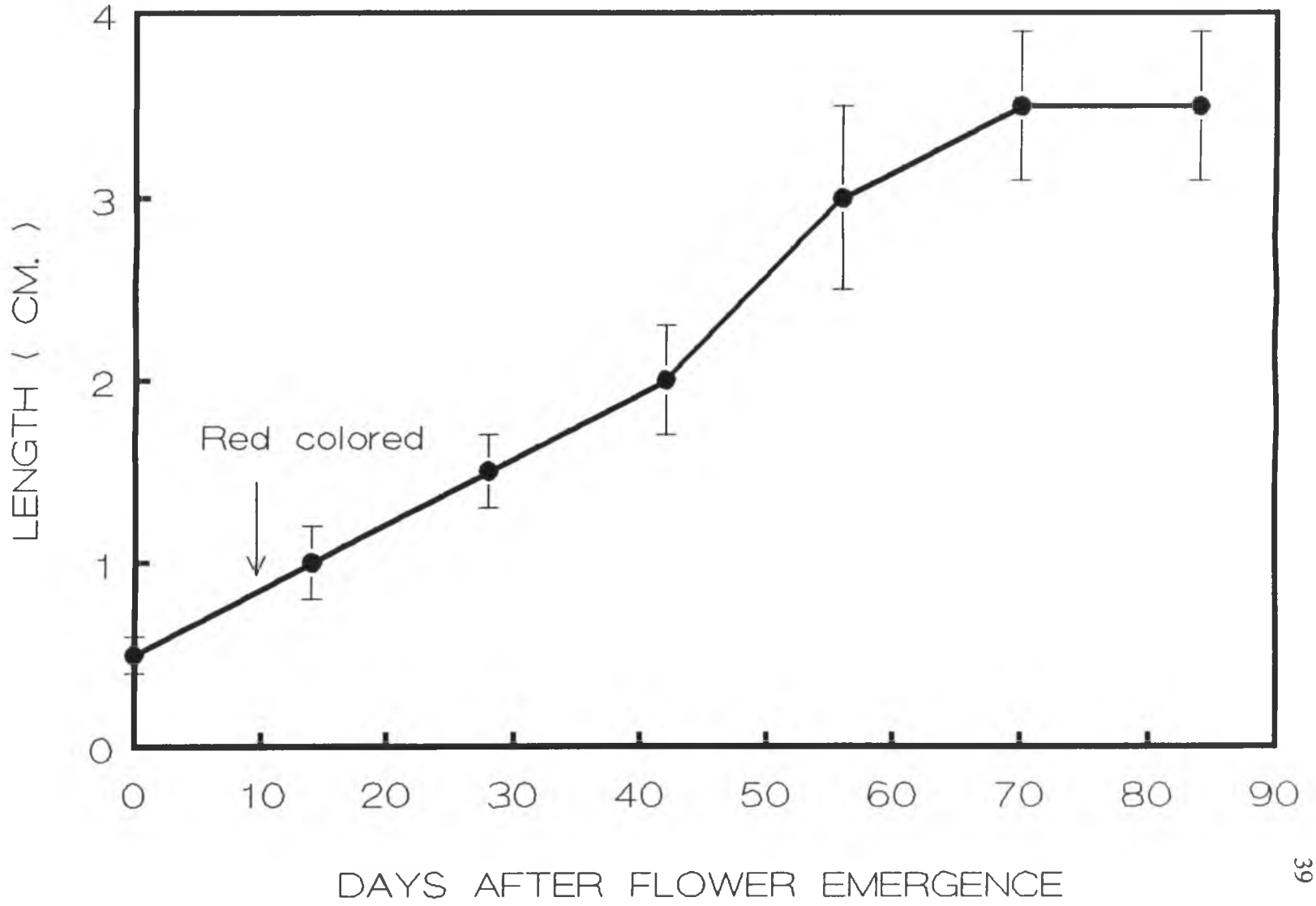
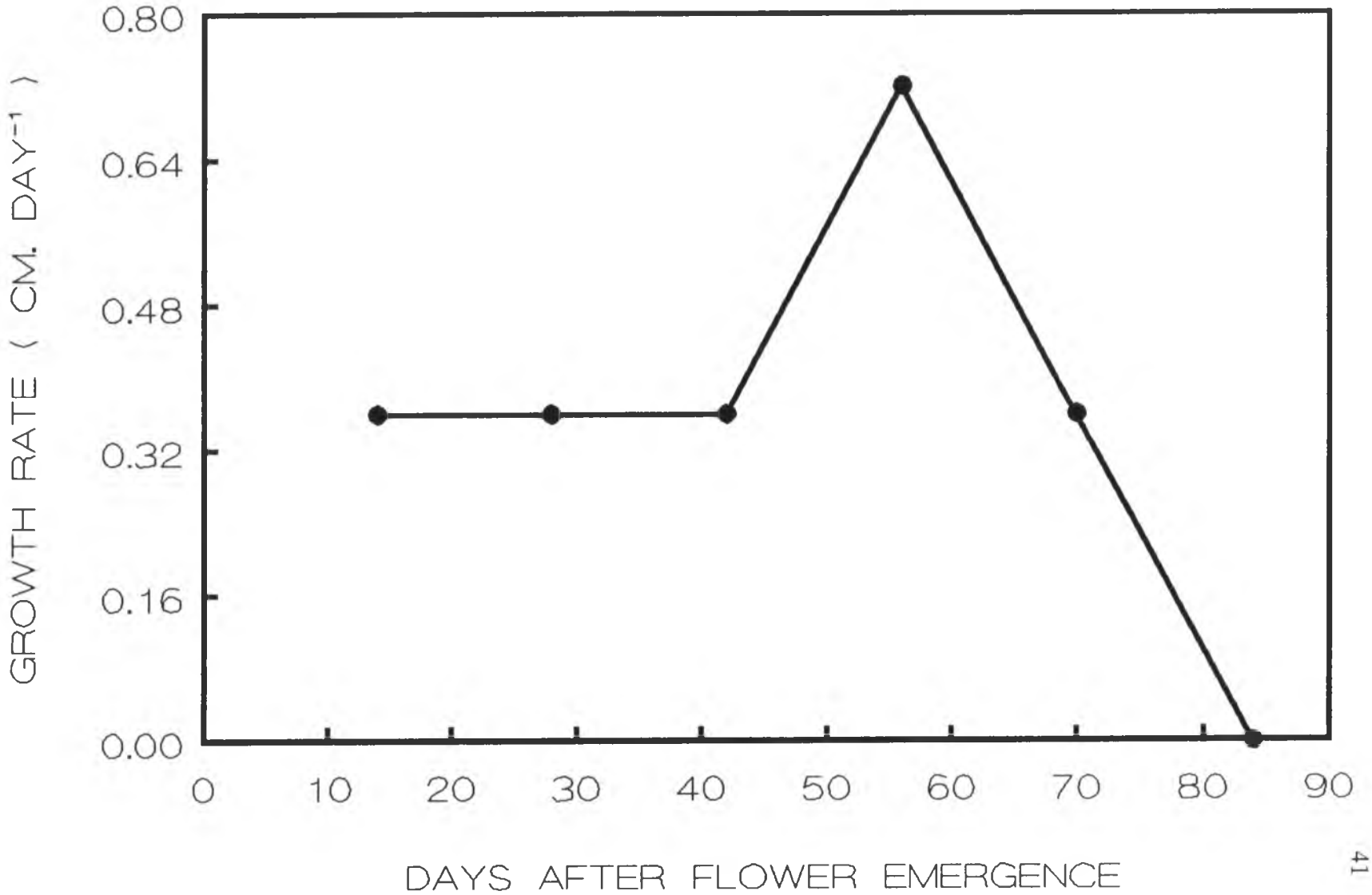

LENGTH (CM.)
4
3
2
1
0
Red colored
0
10
20
30
40
50
60
70
80
90
DAYS AFTER FLOWER EMERGENCE

Figure 5-B. *A. andraeanum* 'Kaumana' flower spathe lobes growth rate after flower emergence. The growth rate was estimated as means of the lobes length changes divided by change in days.


GROWTH RATE (CM. DAY^{-1})
0.80
0.64
0.48
0.32
0.16
0.00
0
10
20
30
40
50
60
70
80
90
DAYS AFTER FLOWER EMERGENCE

Subtending Leaf Growth

Approximately seven days after flower emergence, a new leaf sheath emerged from the old leaf sheath axil. The old leaf sheaths were 11 to 13 cm long. The new leaf sheath elongated very slowly (Figure 6-B) and reached its maximum length of 15 cm at day 21 (Figure 6-A). A new leaf emerged from this sheath (Figure 7-A) and the petiole elongated rapidly, 1.1 cm day^{-1} (Figure 7-B). Seven days after leaf emergence, which was 28 days from flower emergence, the petiole reached its highest elongation rate of 1.9 cm day^{-1}, and then the growth rate decreased slightly for the next seven days. As the petiole approached to its full length, about 21 days after leaf emergence and 42 days from flower emergence, the growth rate declined to 1.0 cm day^{-1}. The leaf petiole continued to elongate very slowly for another 14 to 21 days and stopped 42 days after subtending leaf emergence and 56 days from flower emergence.

Leaf blade growth after emergence was sigmoid (Figure 8-A). At first, the growth rate was 0.15 cm day^{-1} (Figure 8-B) and then increased. At 21 days from leaf emergence, the leaf blade reached its maximum growth rate of 0.9 cm day^{-1}. The growth rate then started to decline for seven days (0.78 cm day^{-1}), then decreased rapidly for the following seven days to 0.11 cm day^{-1}. The leaf blade continued to grow slowly and stopped at day 49 from leaf emergence which was about 70 days from flower emergence (Figure 8-A).

The unfurling of the leaf blade occurred 14 days after leaf emergence (Figure 8-A). The color of the leaf blade at this time was olive brown (Table 1). Seven days later, it became light green and gradually changed to green in 7 days. During this growth period, the texture of the leaf blade was soft. The leaf blade continued growing for another 7 days as it approached full maturity. Color changed to dark green, and the texture of the leaf blade became hard. Seven days later, the leaf blade became fully mature, with a very hard texture and there were no further changes in color.

Seasonal Variations

The seasonal growth variation of 'Kaumana' grown in the glasshouse was shown in Figure 9-A and Figure 10-A. During the winter (from January to April) the flower stalk and leaf petiole were shorter than during the summer (from April to June) (Figure 9-A, 10-A). The maximum flower stalk growth rate was higher from April to June (Figure 10-B). The maximum leaf petiole growth rate was higher during January to April (Figure 9-B). The leaf emerged one week earlier in summer compared to winter (Figure 9-A, 10-A).

Figure 6-A. Leaf sheath growth of *A. andraeanum* 'Kaumana' after previous flower emergence. A leaf was enclosed in the sheath. Data are the mean values of eight to fifteen leaf sheathes from the same number of plants. Bars show the variation of the sheath lengths.

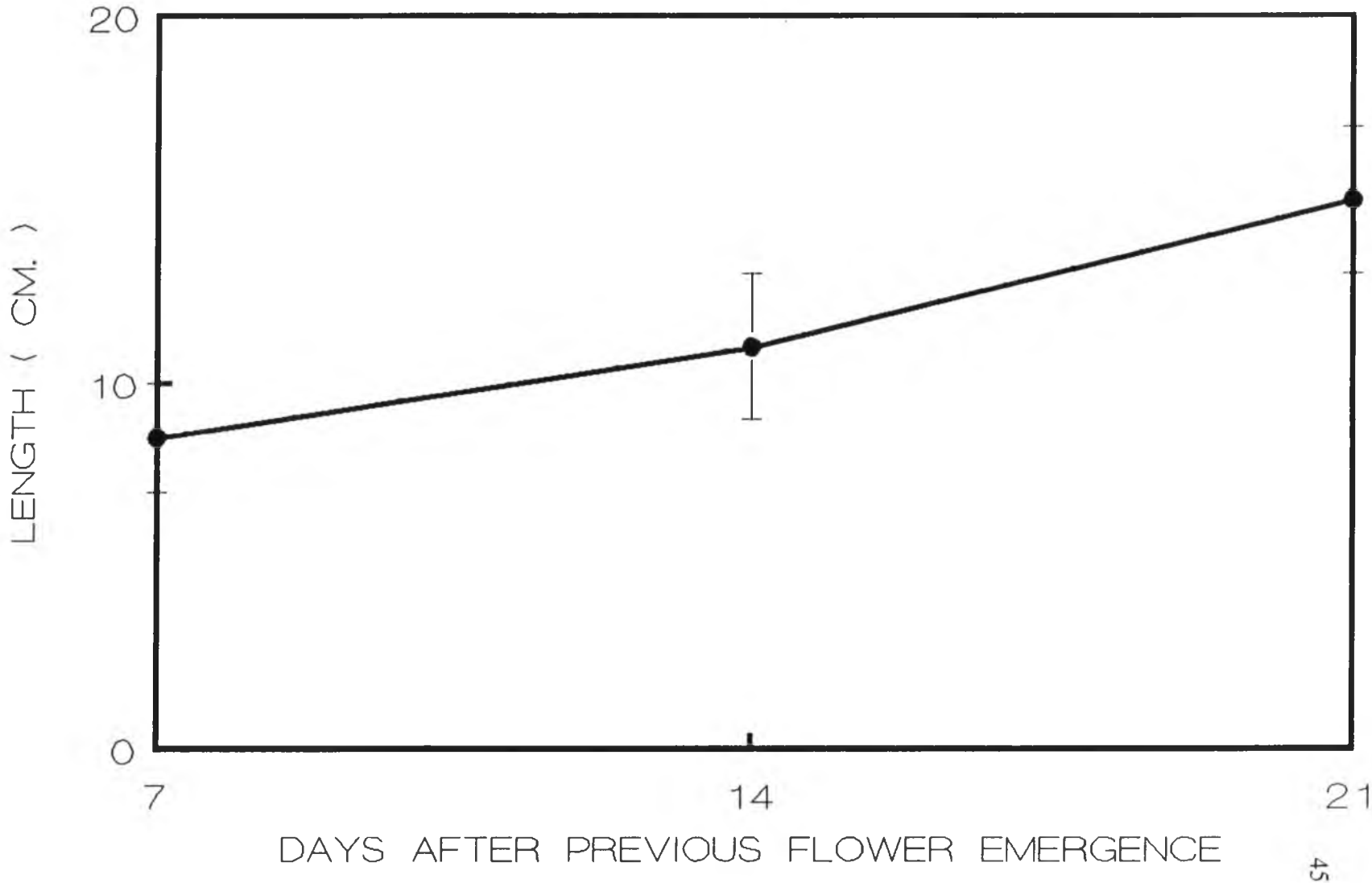

20
10
0
LENGTH (CM.)
7
14
21
DAYS AFTER PREVIOUS FLOWER EMERGENCE

Figure 6-B. Leaf sheath growth rate of *A. andraeanum* 'Kaumana' after previous flower emergence. The growth rate was estimated as means of sheath length changes divided by change in days.

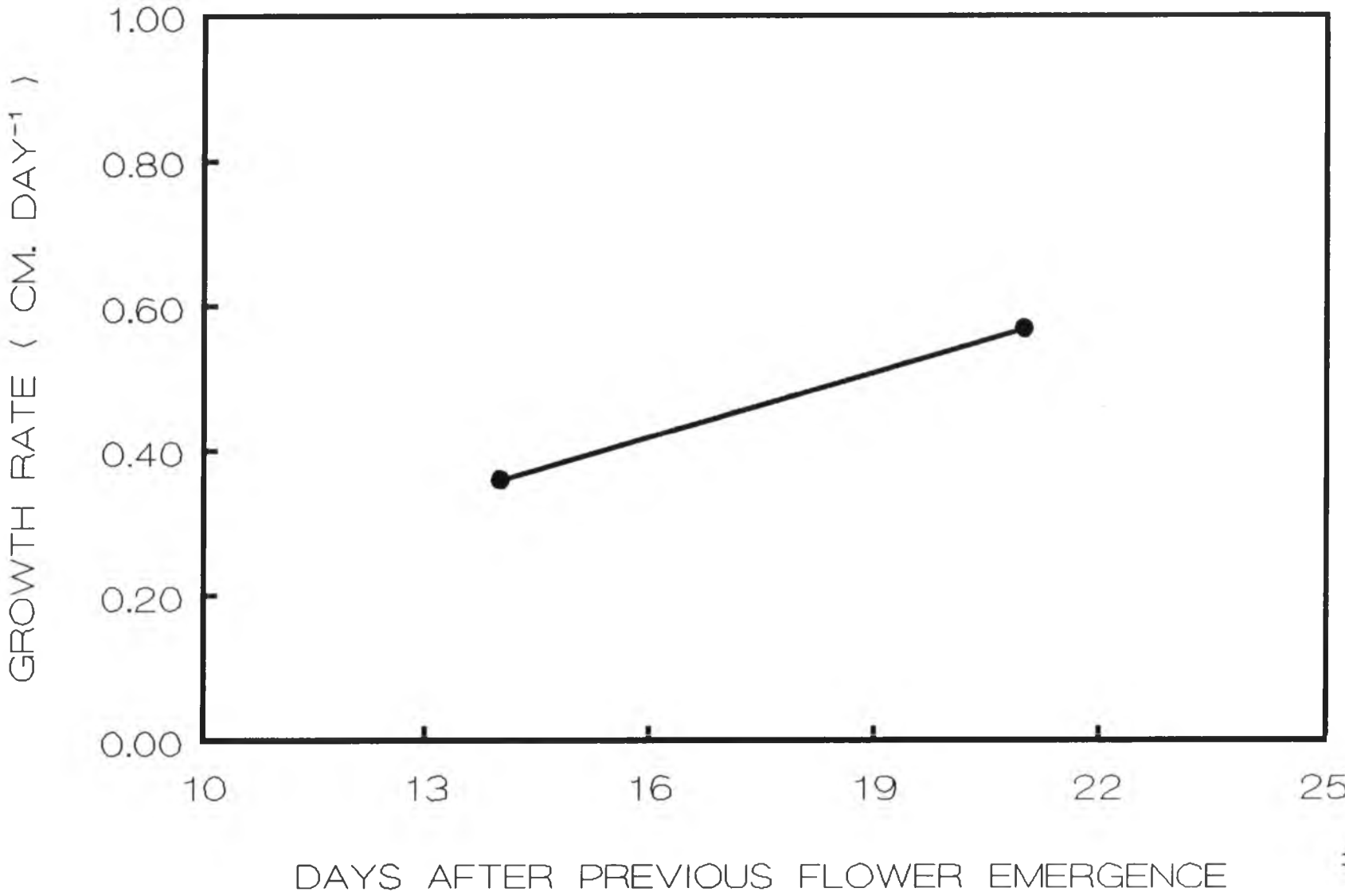

1.00
0.80
0.60
0.40
0.20
0.00
GROWTH RATE (CM. DAY-1)
10
13
16
19
22
25
DAYS AFTER PREVIOUS FLOWER EMERGENCE

Figure 7-A. Subtending leaf petiole growth of *A. andraeanum* 'Kaumana' after emergence during January to April, 1988. Subtending leaf emerged about 21 days after previous flower emergence and were bearing the next flower bud inside its petiole base. Data are the mean values of leaves on eight to fifteen plants. Bars show the variation of the petiole lengths.

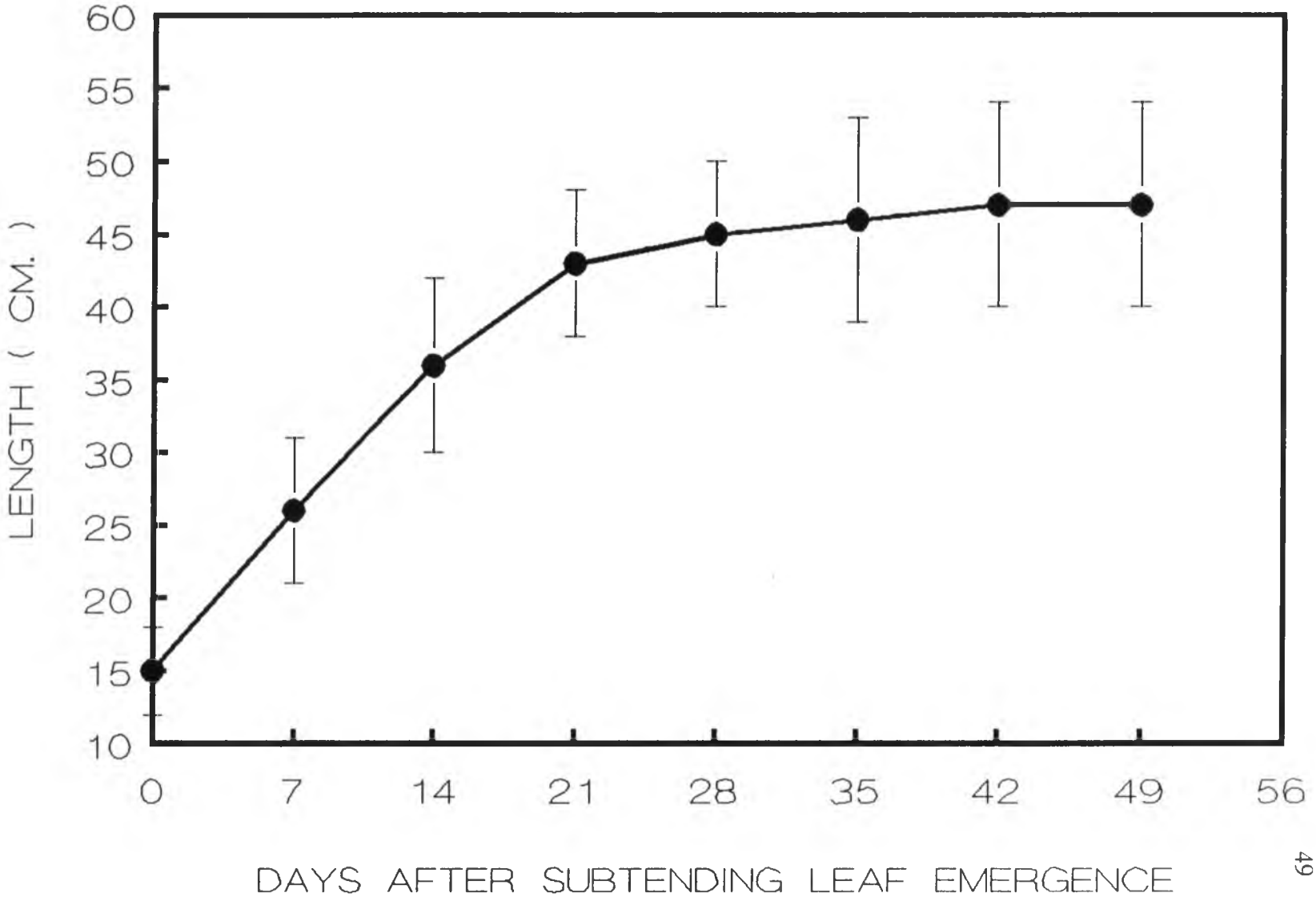

LENGTH (CM.)
60
55
50
45
40
35
30
25
20
15
10
0
7
14
21
28
35
42
49
56
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 7-B. Subtending leaf petiole growth rate of *A. andraeanum* 'Kaumana' after emergence during January to April, 1988. The growth rate was estimated as means of petiole length changes divided by change in days.

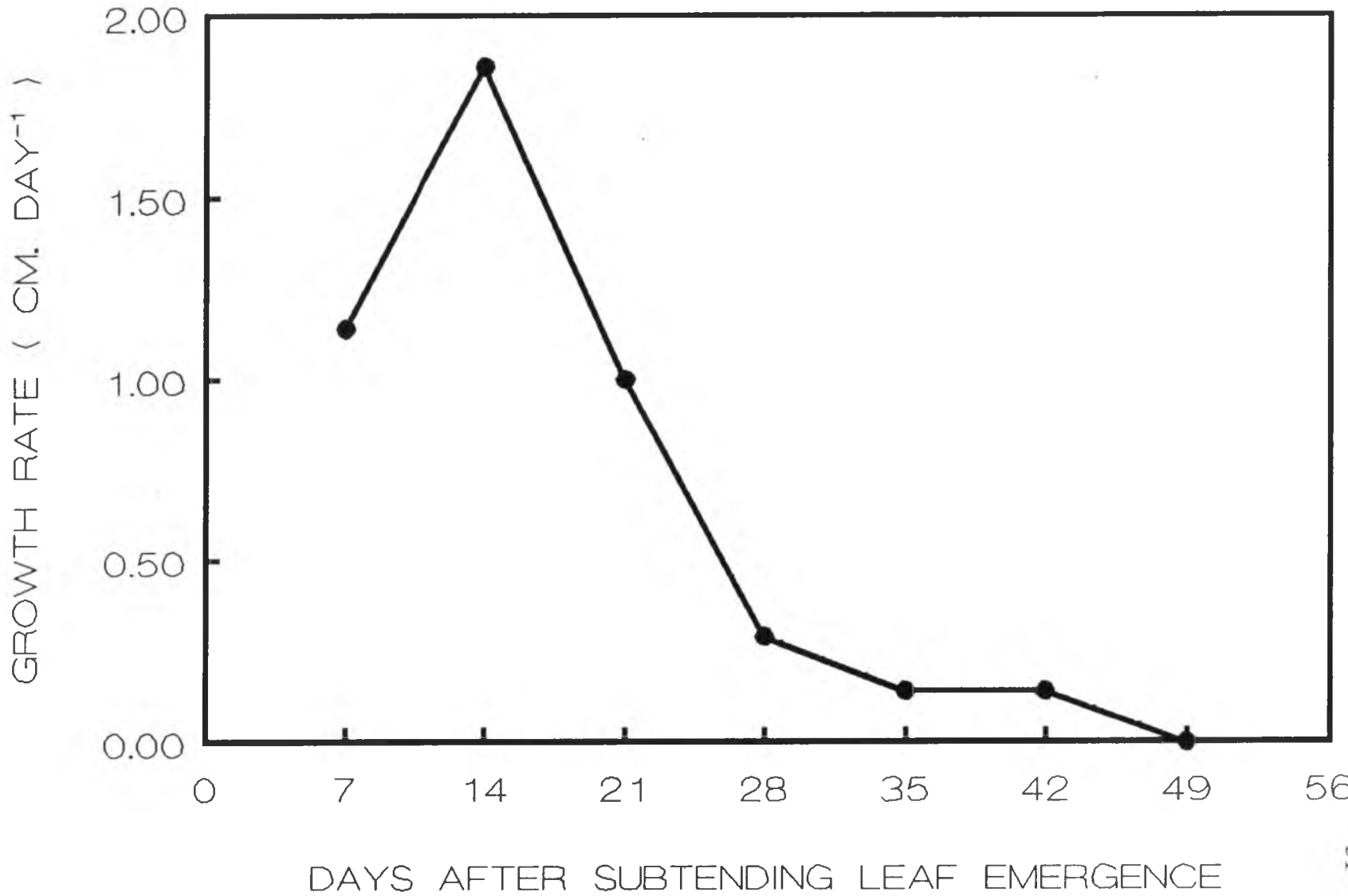

2.00
1.50
1.00
0.50
0.00
GROWTH RATE (CM. DAY^{-1})
0
7
14
21
28
35
42
49
56
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 8-A. Subtending leaf blade growth of A. andraeanum 'Kaumana' after emergence during January to April, 1988. Leaf blade color changed along with the growth. Data are the mean values of leaves on eight to fifteen plants. Bars show variation of the leaf blade lengths.

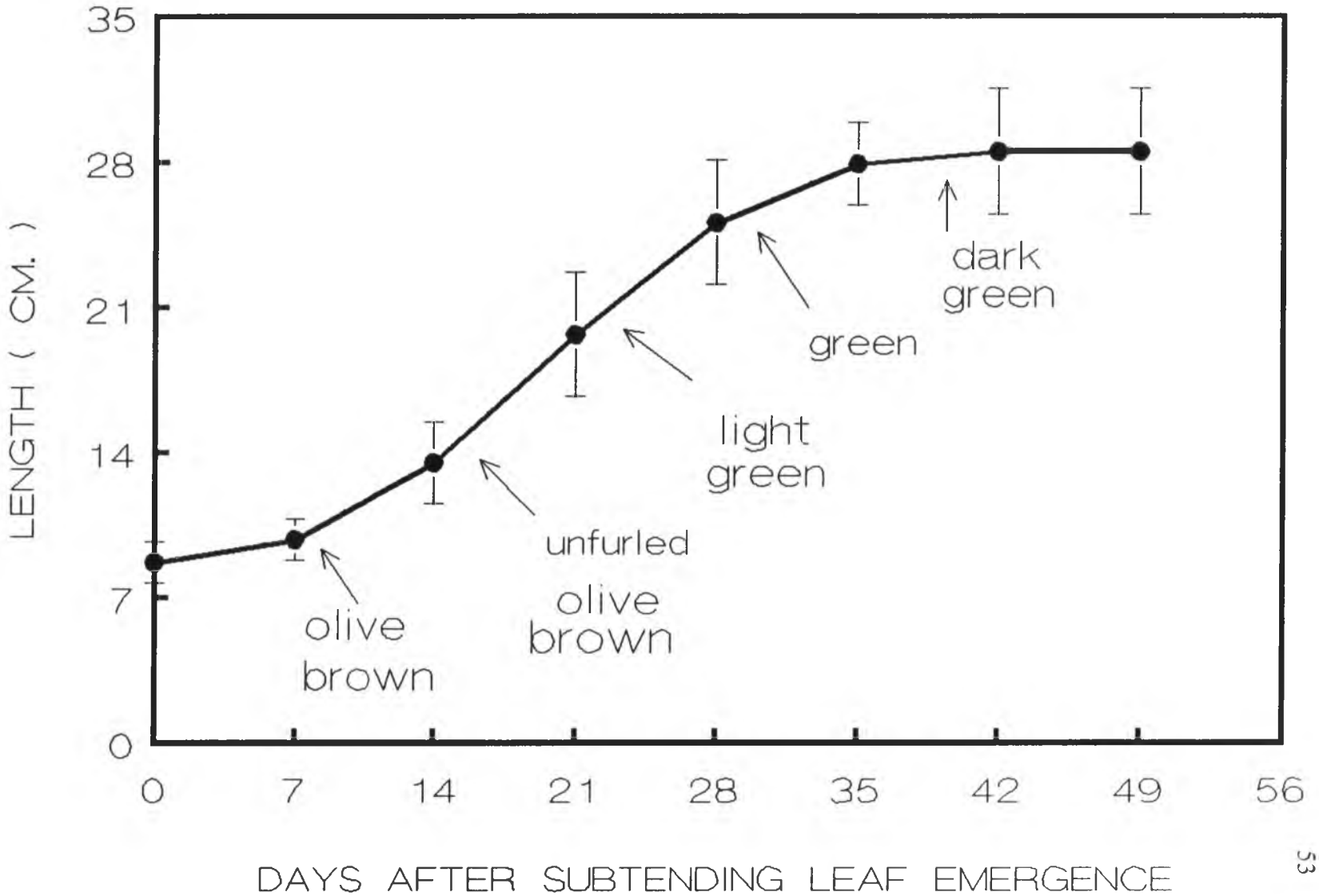

35
28
21
14
7
0
LENGTH (CM.)
0
7
14
21
28
35
42
49
56
DAYS AFTER SUBTENDING LEAF EMERGENCE
olive brown
unfurled
olive brown
light green
green
dark green

Figure 8-B. Subtending leaf blade growth rate of *A. andraeanum* 'Kaumana' after emergence during January to April, 1988. The growth rate was estimated as means of leaf blade length changes divided by change in days.

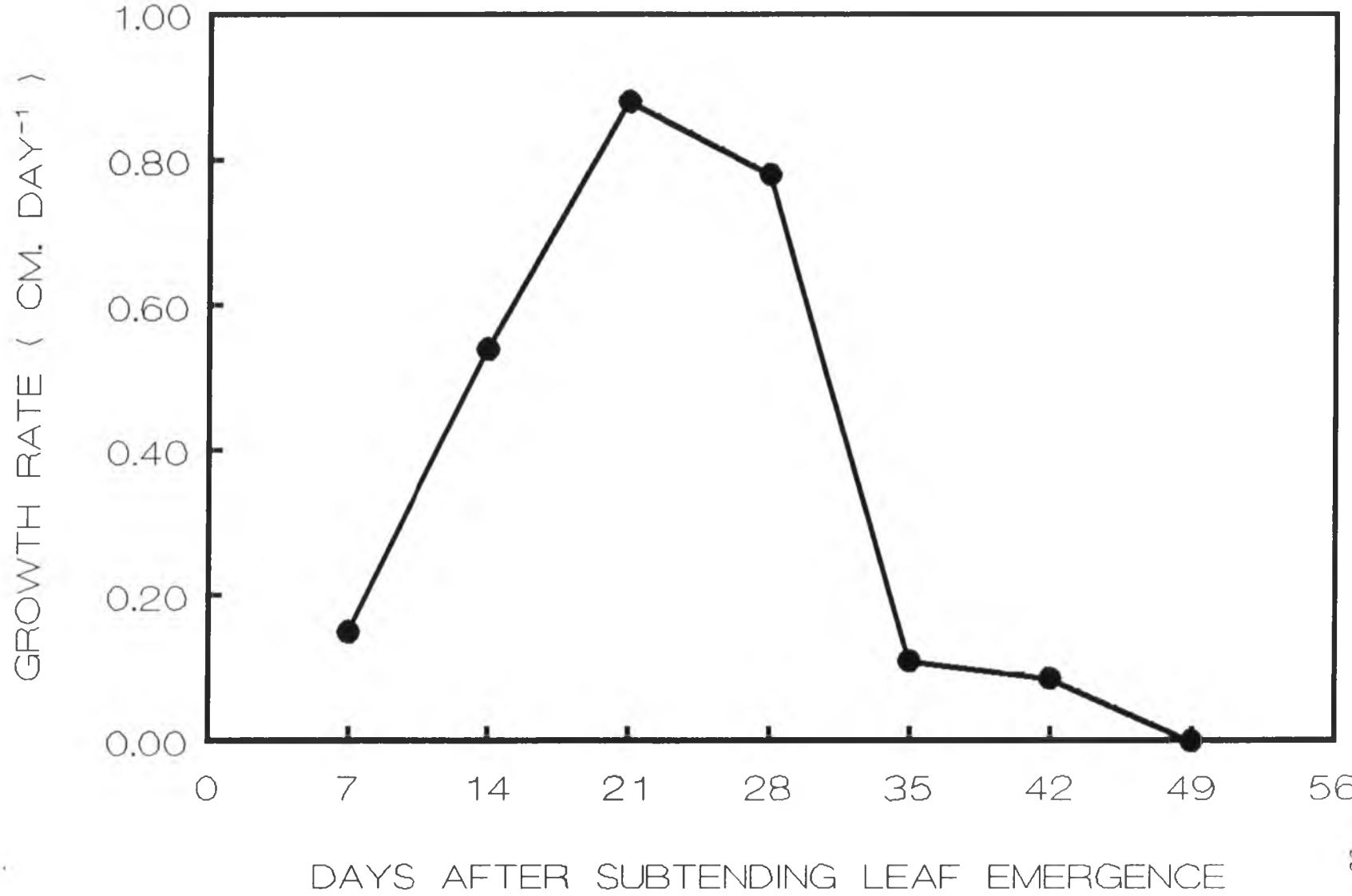

GROWTH RATE (CM. DAY-1)
1.00
0.80
0.60
0.40
0.20
0.00
0
7
14
21
28
35
42
49
56
DAYS AFTER SUBTENDING LEAF EMERGENCE

Table 1. Leaf color and texture during emergence and unfurling of the leaf blade.

Time from emergence (days)	Color	Y[a]	x	y	Texture
35	olive brown	18.2	0.363	0.436	crispy
42	light green	20.9	0.382	0.501	soft
49	green	29.3	0.357	0.496	hard
56	dark green	30.0	0.325	0.491	very hard

[a] leaf blade color were determined according to the *R.H.S. Colour Chart* (Royal Hort. Soc. Colour Chart, 1966).

Figure 9-A. Flower stalk, leaf sheath, and leaf petiole elongation of *A. andraeanum* 'Kaumana' from January to April, 1988. Daytime temperatures were 20^{o} to 22^{o}C and night temperatures were 16^{o} to 18^{o}C. The average photon flux density was 55 uE m^{-2} sec^{-1}. Data are the mean values of flowers and leaves on eight plants. Bars show the variation of the lengths.

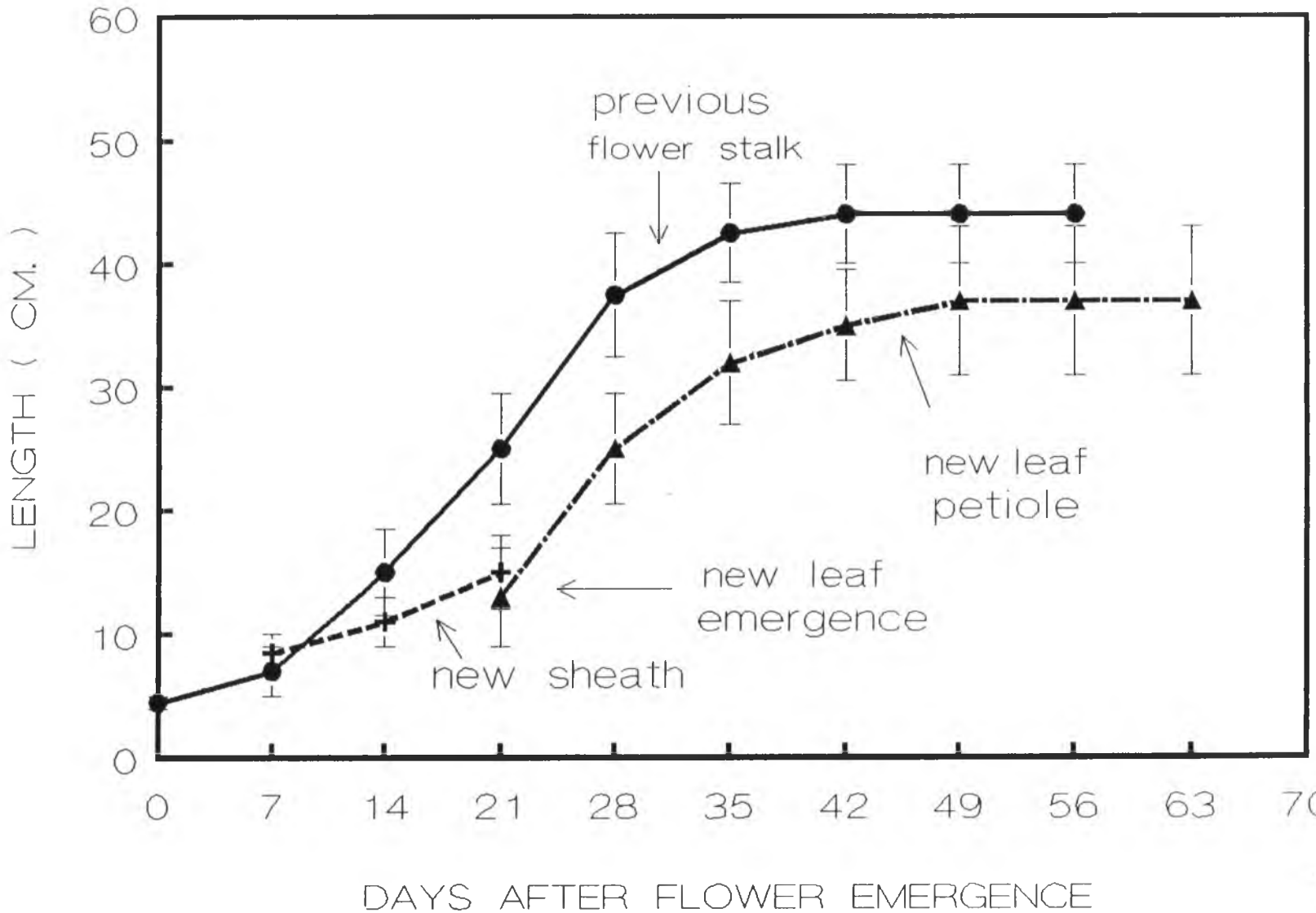

60
50
40
30
20
10
0
LENGTH (CM.)
previous
flower stalk
new leaf
petiole
new leaf
emergence
new sheath
0
7
14
21
28
35
42
49
56
63
70
DAYS AFTER FLOWER EMERGENCE

Figure 9-B. Growth rate of flower stalk, leaf sheath, and leaf petiole of *A. andraeanum* 'Kaumana' from January to April, 1988. Daytime temperatures were 20^{o} to 22^{o}C and night temperatures were 16^{o} to 18^{o}C. The average photon flux density was 55 uE m^{-2} sec^{-1}. Growth rate was determined as change in length divided by change in days.

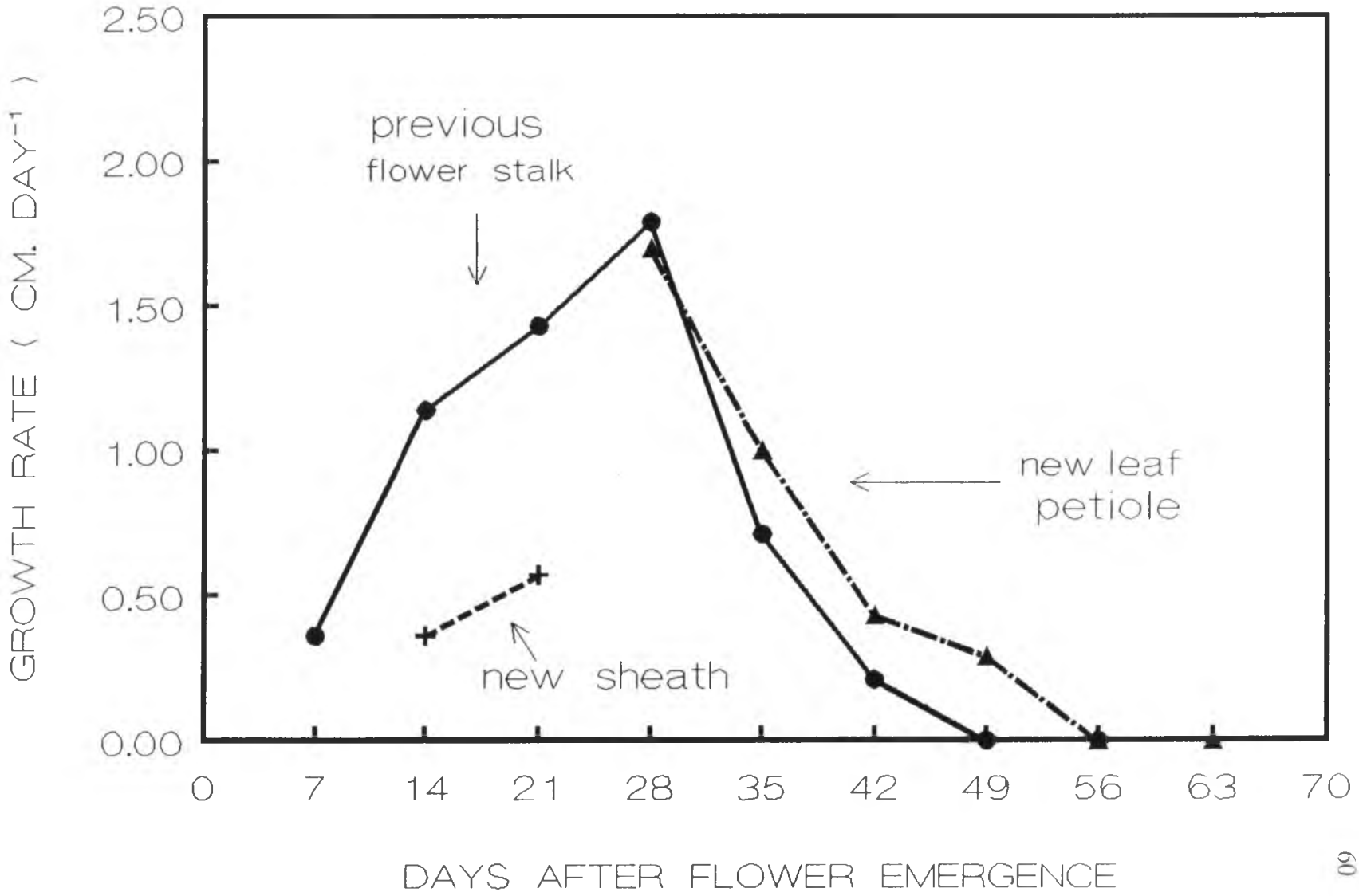

GROWTH RATE (CM. DAY^{-1})
2.50
2.00
1.50
1.00
0.50
0.00
previous
flower stalk
new leaf
petiole
new sheath
0
7
14
21
28
35
42
49
56
63
70
DAYS AFTER FLOWER EMERGENCE

Figure 10-A. Flower stalk, leaf sheath, and leaf petiole elongation of *A. andraeanum* 'Kaumana' from April to June, 1988. Daytime temperatures were 24^{o} to 28^{o}C and night temperatures were 20^{o} to 22^{o}C. The average photon flux density was 70 uE m^{-2} sec^{-1}. Data are the mean values of flowers and leaves on eight plants. Bars show the variation of the lengths.

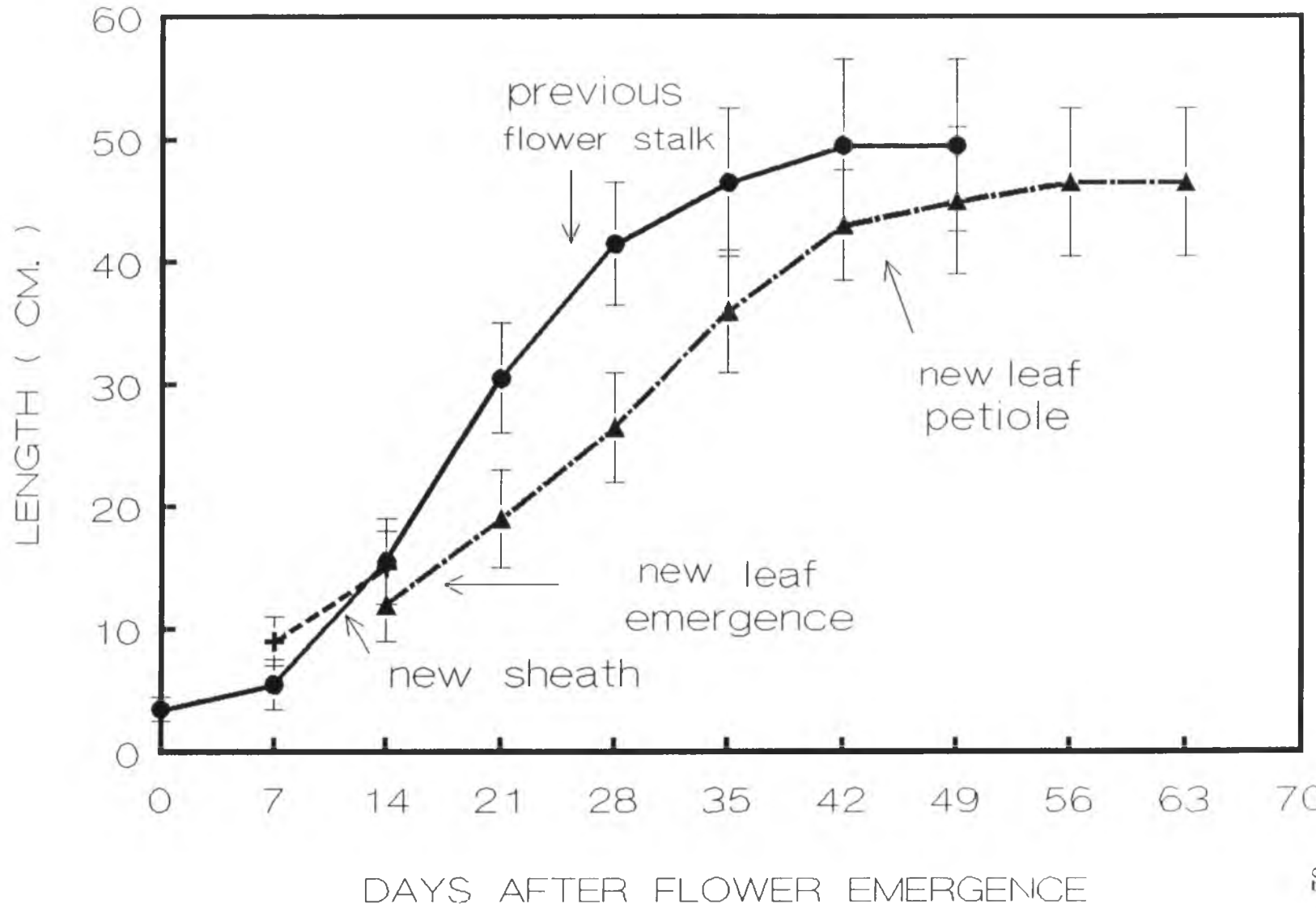
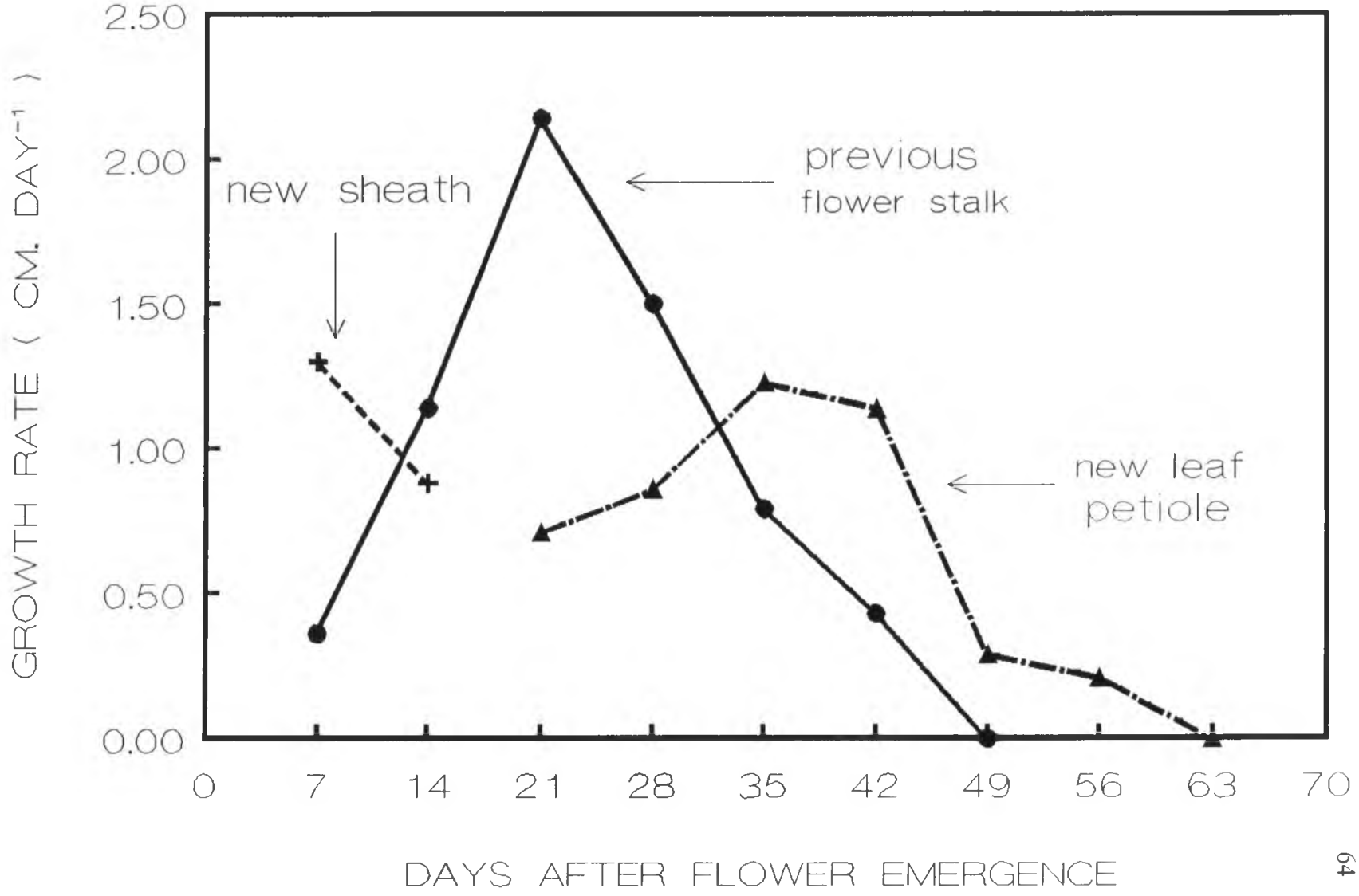

60
50
40
30
20
10
0
LENGTH (CM.)
previous
flower stalk
new leaf
petiole
new leaf
emergence
new sheath
0
7
14
21
28
35
42
49
56
63
70
DAYS AFTER FLOWER EMERGENCE

Figure 10-B. Growth rate of flower stalk, leaf sheath, and leaf petiole of *A. andraeanum* 'Kaumana' during April to June, 1988. Daytime temperatures were 24^{o} to 28^{o}C and night temperatures were 20^{o} to 22^{o}C. The average photon flux density was 70 uE m^{-2} sec^{-1}. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (CM. DAY-1)
2.50
2.00
1.50
1.00
0.50
0.00
0
7
14
21
28
35
42
49
56
63
70
DAYS AFTER FLOWER EMERGENCE
new sheath
previous
flower stalk
new leaf
petiole

Flower Bud Growth And Development Inside The Subtending Leaf Petiole Base

Flower Bud Growth And Development

During the period when the young flower was visible at the base of the petiole, another new leaf (about 3.5 cm long from petiole base to leaf tip) was growing inside the new leaf sheath. Inside the petiole base of this new leaf, a new small flower bud was developing. The smallest flower bud which was measurable was about 0.3 cm long and still had active cell division as detected by an acetocarmine smear for showing mitotic figures. Before subtending leaf emergence, flower bud growth started and its length (from stem base to spathe tip) increased from 0.4 $\pm$0.1 cm to 0.8 $\pm$0.1 cm in about 21 days (Figure 11-A). When the new leaf was about to emerge from its sheath, the length of the flower bud was 0.9 cm, 15% of its emergence length. The growth rate of this period was 0.22 mm day^{-1} (Figure 11-B). At the day of subtending leaf emergence to day 14 after leaf emergence, flower bud growth stopped with the length remaining 1.0 $\pm$0.1 cm (Figure 11-A), approximately 20% of the emergence length. The growth rate was 0.07 mm day^{-1} (Figure 11-B). Microscopic observation showed few mitotic figures at this stage. Vascular tissue was obvious now, and stomata were observed at this stage. After this stage, flower bud growth recommenced (Figure 11-A) and gradually

Figure 11-A. *A. andraeanum* 'Kaumana' flower bud growth inside the petiole base before emergence. The age of the flower bud was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in length. Data are the mean values of flower buds from eight plants. Bars are the variation of the flower bud lengths.

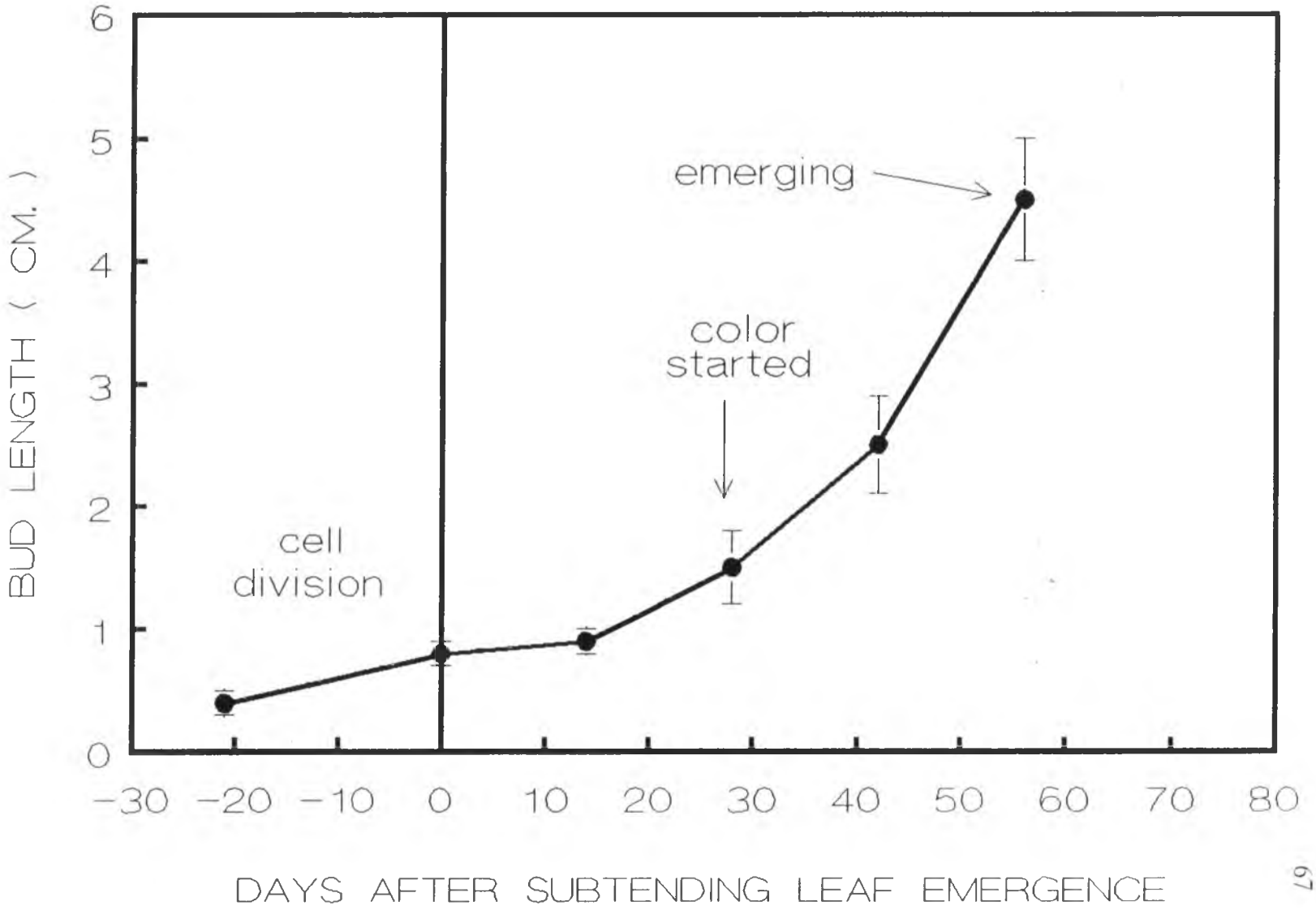
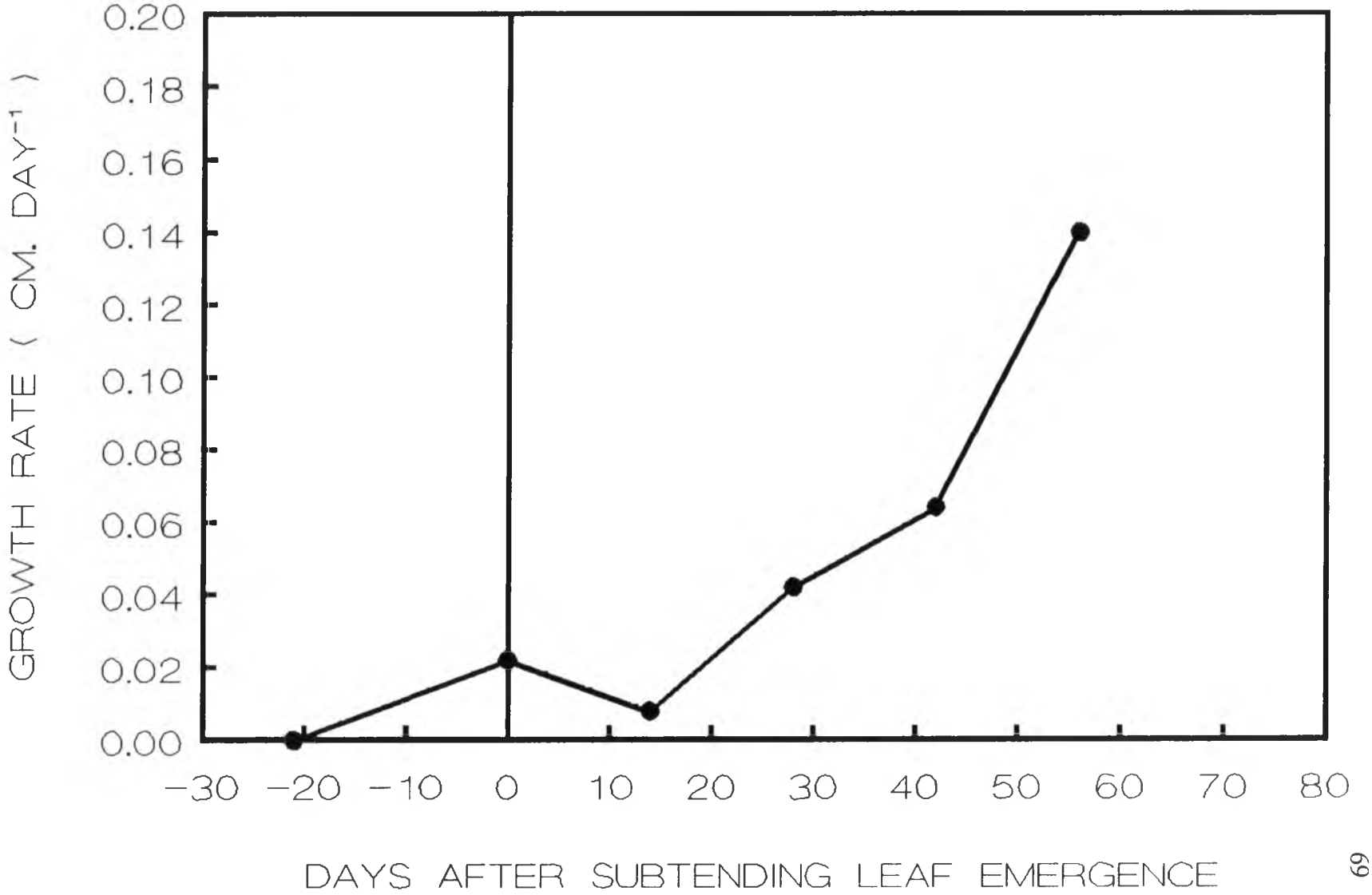

BUD LENGTH (CM.)
0
1
2
3
4
5
6
cell
division
color
started
emerging
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 11-B. *A. andraeanum* 'Kaumana' flower bud growth rate inside the subtending leaf petiole base before emergence. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (CM. DAY-1)
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
-30 -20 -10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

increased from 0.9 to 1.5 cm with a growth rate of 0.43 mm day^{-1} (Figure 11-B). This was 28 days after subtending leaf emergence and 28 days before flower emergence. From day 28 to day 42 after leaf emergence which was between 28 days to 14 days before flower emergence, the flower bud grew very fast and increased from 1.5 to 2.5 cm with a growth rate of 0.64 mm day^{-1}. This was approximately 50% of its emergence length. Anthocyanins synthesis began at this period, and the spathe showed noticeable red color. Flower bud growth rate reached 1.4 mm day^{-1} as the bud increased from 50% to 100% of the emergence length (4.5 to 5.0 cm). At this stage, 80% of the spathe length was brightly colored, and the bud was poised to emerge from the petiole base. This was 56 days after subtending leaf emergence (Figure 11-A).

Spathe Growth And Development Before Flower Emergence

The first part of the flower to grow rapidly was the spathe (Figure 12-A) since flower bud was 0.4 $\pm$0.1 cm long. Twenty one days before leaf emergence, when the flower bud was 0.4 $\pm$0.1 cm long, the spathe had a length of 0.3 $\pm$0.1 cm (Figure 12-A), and occupied 75% of the bud length. The spathe length started to increase and reached 0.7 cm (Figure 12-A) when the subtending leaf was emerging. The growth rate was 0.19 mm day^{-1} (Figure 12-B) during this period, then declined after leaf emergence. While the flower bud remained at 0.8 to 0.9 cm long, the spathe remained at 0.7 to 0.8 cm long (Figure 11-A, 12-A) from the day of leaf

Figure 12-A. *A. andraeanum* 'Kaumana' flower bud spathe growth inside the petiole base before emergence. The age of the flower bud spathe was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in length. Data are the mean values of flower buds from eight plants. Bars are the variation of the flower bud spathe lengths.

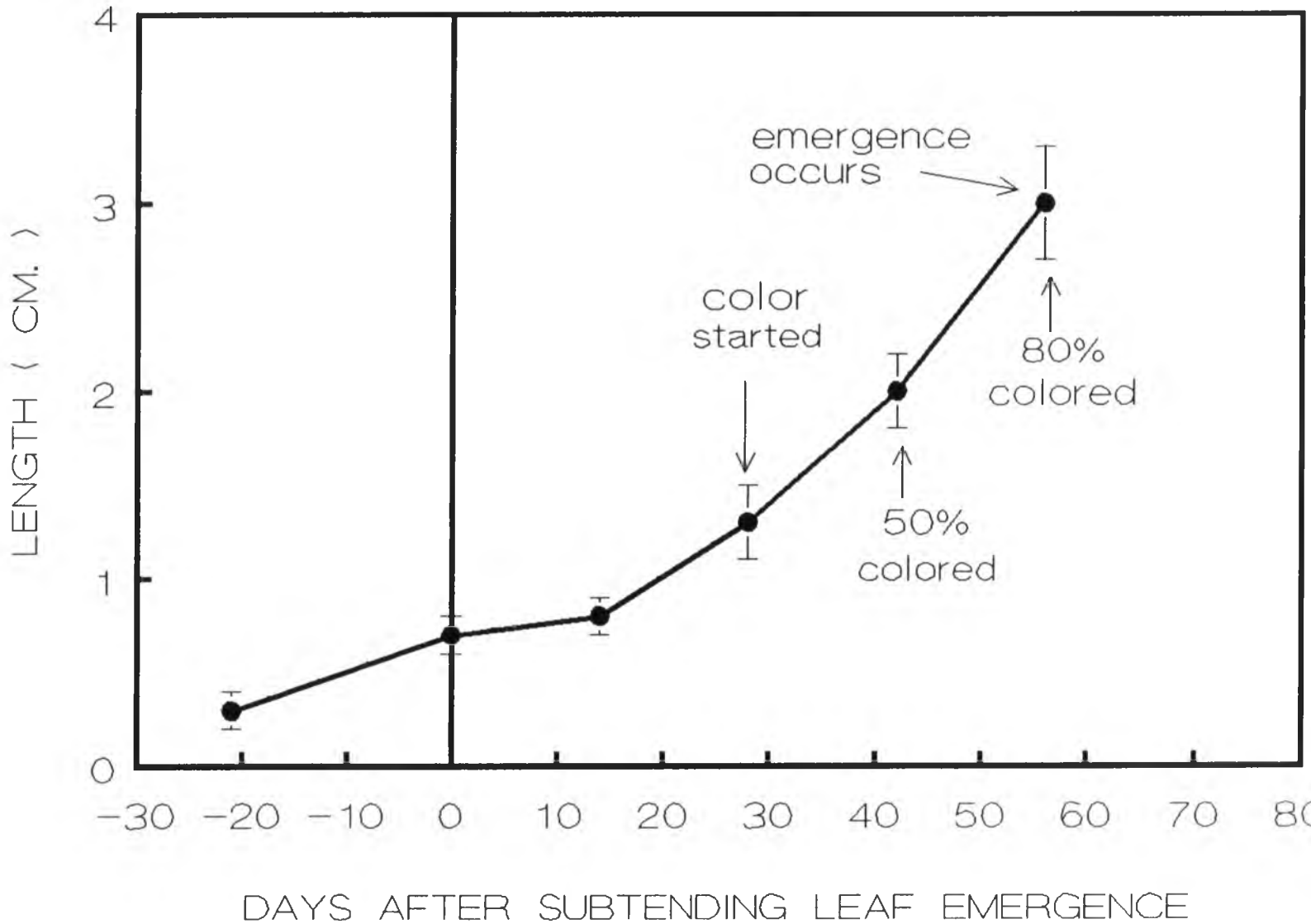
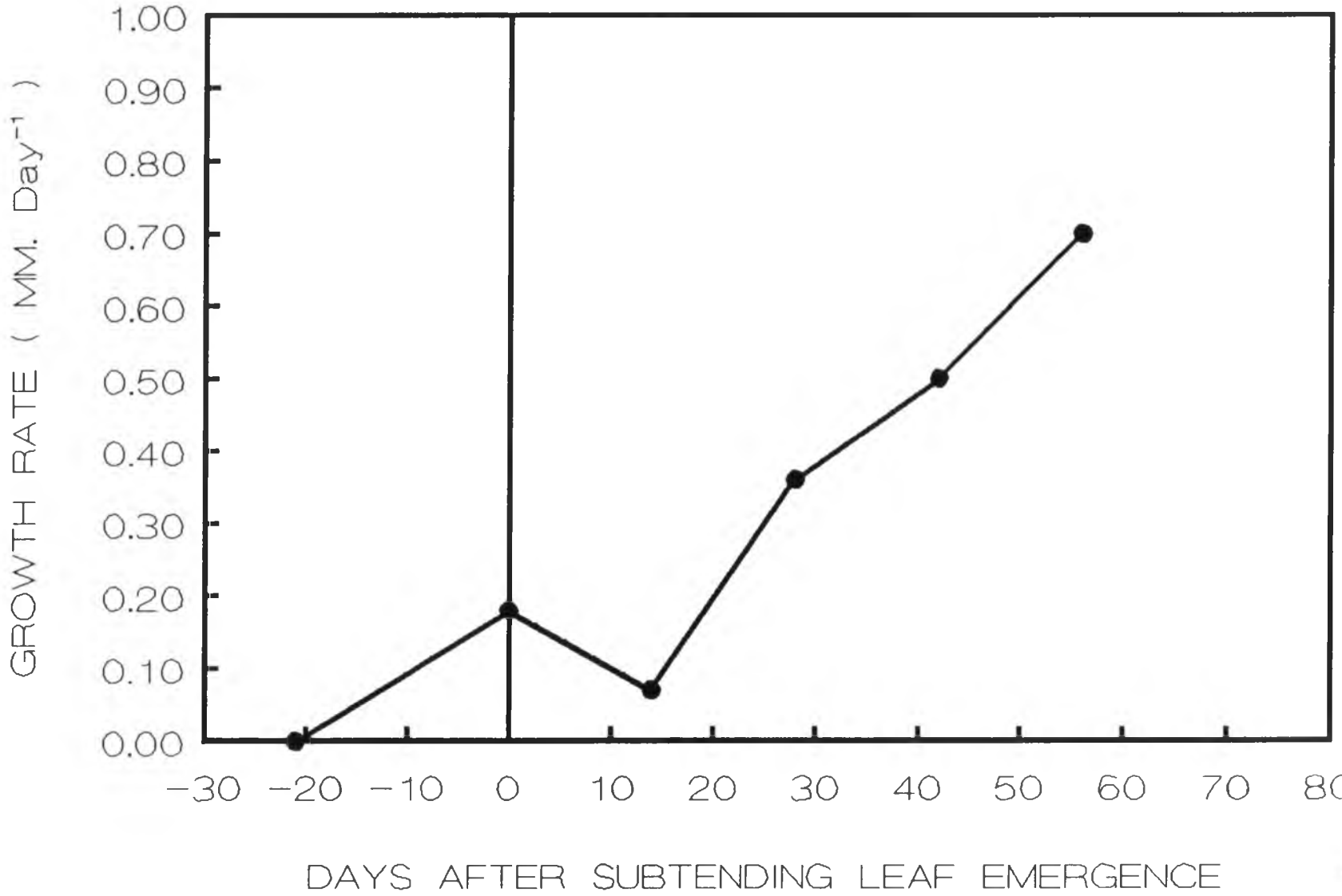

4
3
2
1
0
LENGTH (CM.)
emergence
occurs
color
started
80%
colored
50%
colored
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 12-B. *A. andraeanum* 'Kaumana' flower bud spathe growth rate inside the subtending leaf petiole base before emergence. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (MM. Day⁻¹)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

emergence to day 14 after leaf emergence, and the spathe growth rate was low, only 0.07 mm day^{-1} (Figure 12-B). After this slow growth period, spathe started to grow rapidly, from 0.7 cm to 1.3 cm in 14 days (Figure 12-A) with a growth rate of 0.36 mm day^{-1} (Figure 12-B). The spathe continued to grow, with a growth rate of 0.5 mm day^{-1}, reached to 2 cm in another 14 days. During this period, anthocyanin synthesis started, spathe was from slightly red colored to about 50% red. The spathe continued to grow, with a growth rate of 0.7 mm day^{-1} (Figure 12-B), reached to 3 cm long (Figure 12-A) when the flower bud was going to emerge. At this time, 80% to 90% of the spathe was red, with only the lobe being white. Both growth and growth rate curves of spathe width were similar to spathe length's (Figure 13-A and 13-B).

The two lobes started to grow when the flower bud was about 1.5 cm long, which was about 28 days before flower emergence (Figure 14-A). The shortest lobe length which could be measured was about 0.05 cm. The growth rate increased dramatically after the lobes formed (Figure 14-B). When the flower bud was 2.5 cm long (14 days before flower emergence), the lobe length and width were about the same, 0.2 cm (Figure 14-A) with no color being visible. By the end of full flower development, both lobe length and width reached to about 0.5 cm long and approximately 20% of the spathe length and 30% of the spathe width. But the color on lobe had not developed.

Figure 13-A. *A. andraeanum* 'Kaumana' flower bud spathe width increase inside the petiole base before emergence. The age of the flower bud spathe was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in width. Data are the mean values of flower buds from eight plants. Bars are the variation of the flower bud spathe widths.

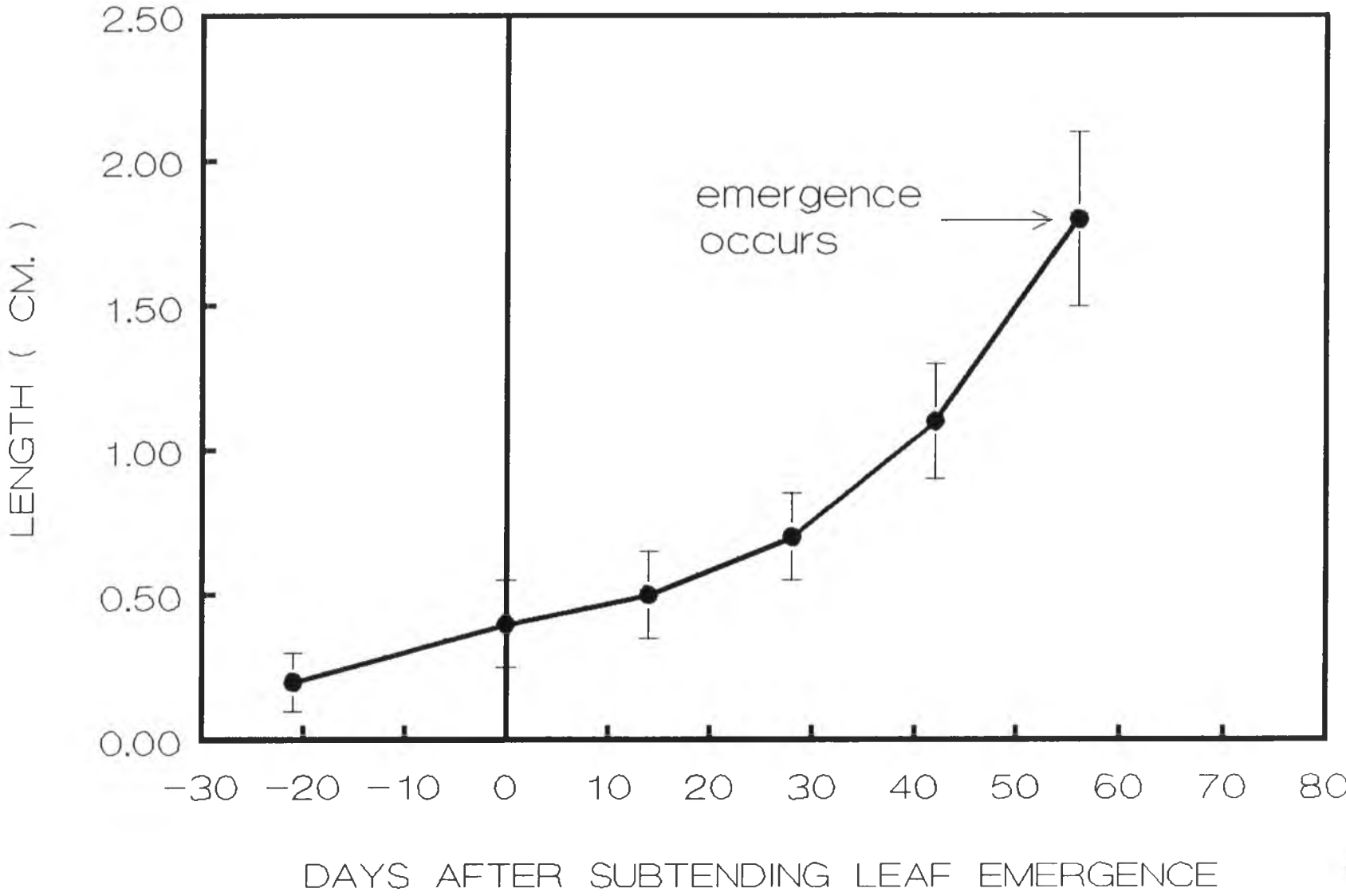

2.50
2.00
1.50
1.00
0.50
0.00
LENGTH (CM.)
emergence
occurs
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 13-B. *A. andraeanum* 'Kaumana' flower bud spathe width growth rate inside the subtending leaf petiole base before emergence. Growth rate was determined as change in width divided by change in days.

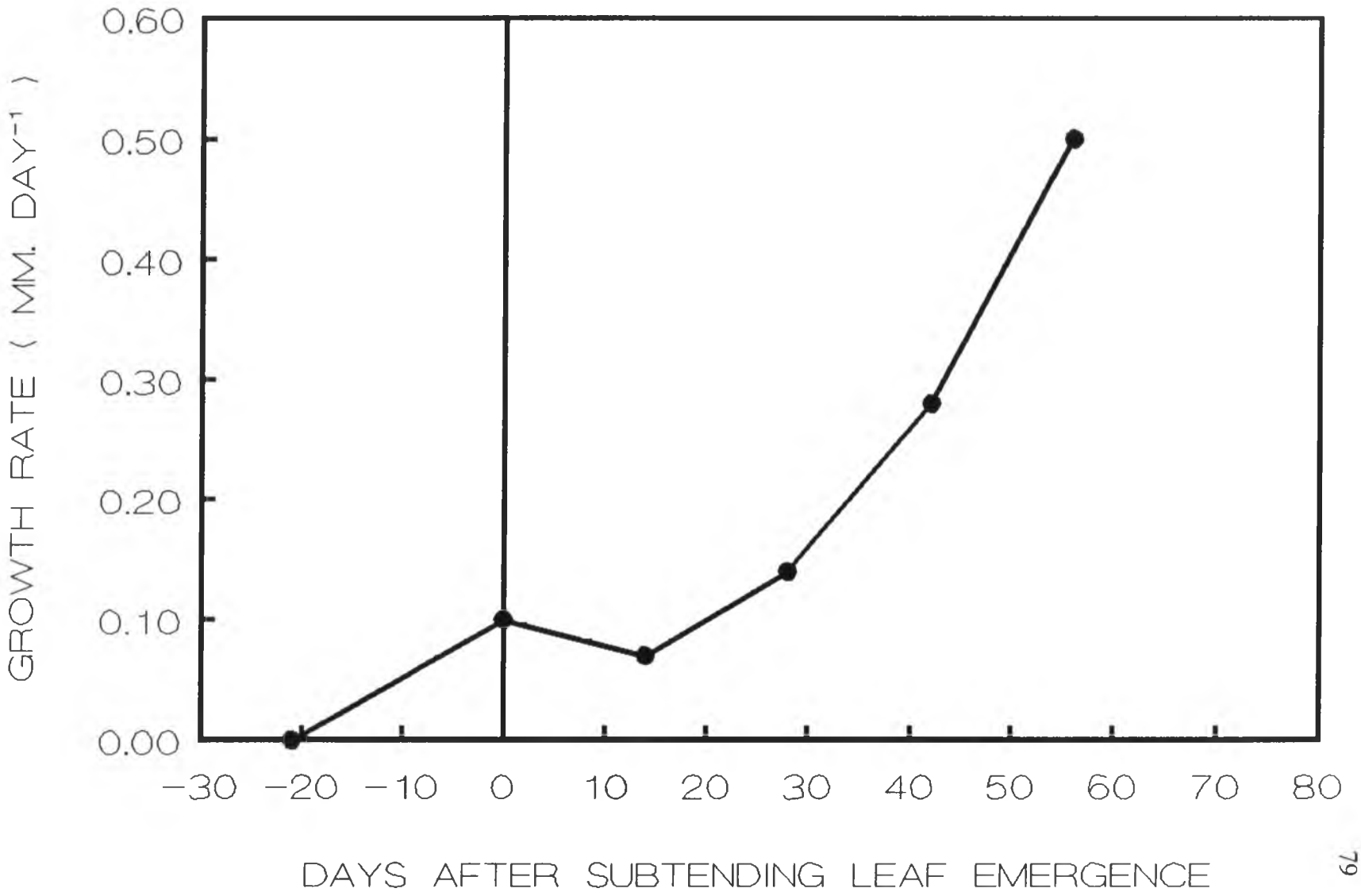

GROWTH RATE (MM. DAY^{-1})
0.60
0.50
0.40
0.30
0.20
0.10
0.00
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 14-A. *A. andraeanum* 'Kaumana' flower spathe lobe growth inside the petiole base before emergence. The age of the lobe was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in lobe length. Data are the mean values of flower buds from eight plants. Bars are the variation of the lobe lengths.

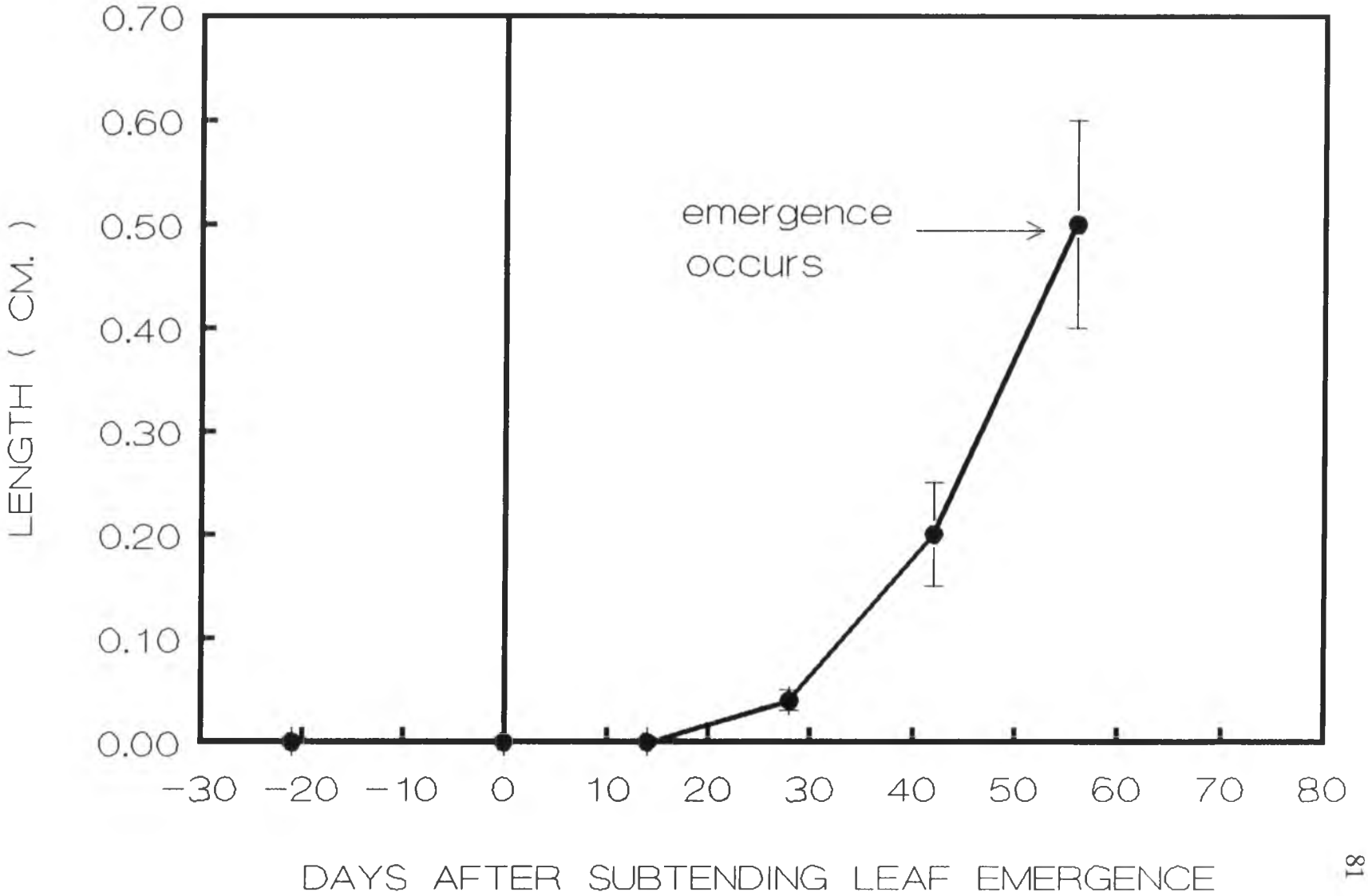
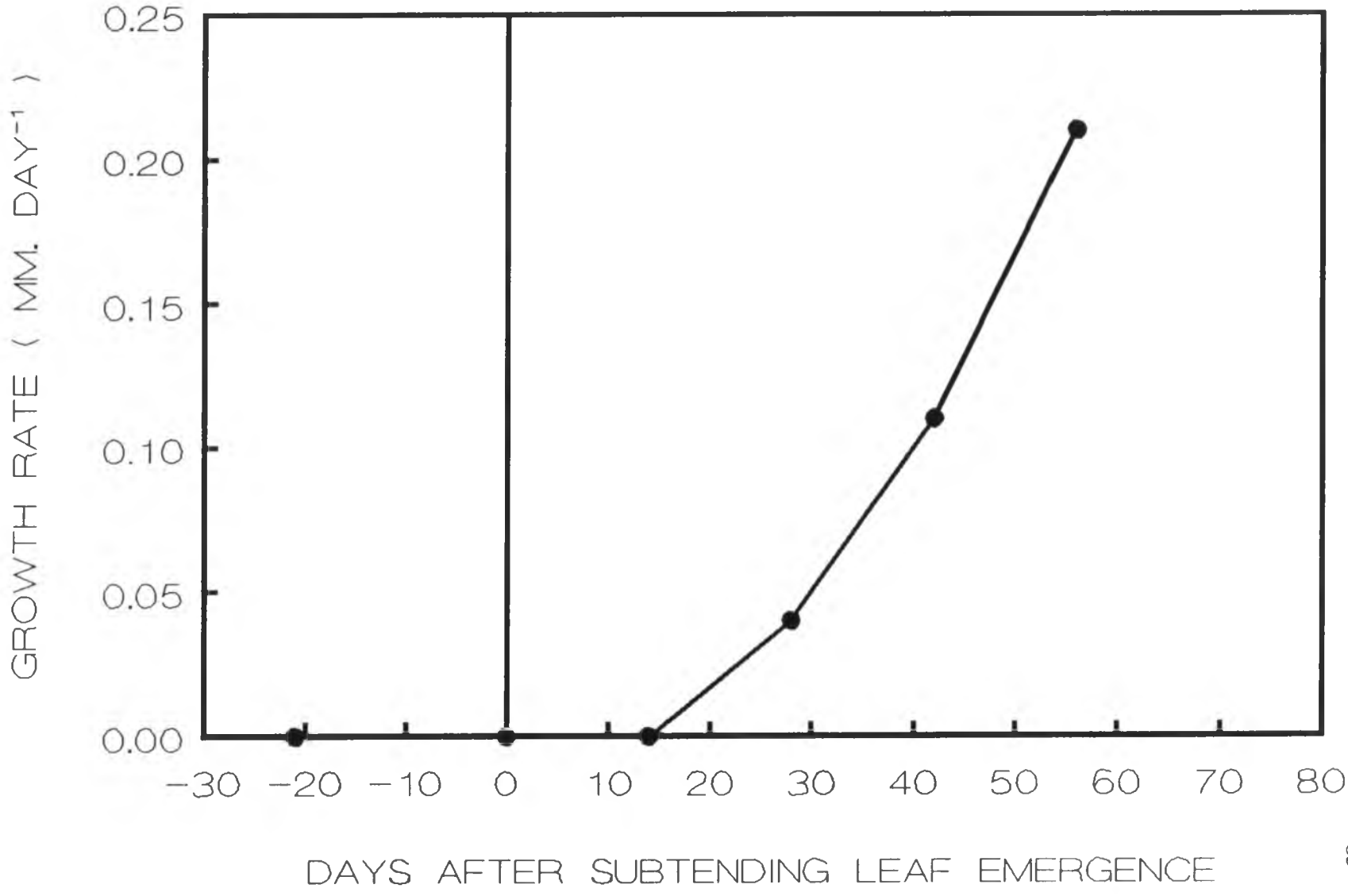

0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
LENGTH (CM.)
emergence
occurs
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 14-B. *A. andraeanum* 'Kaumana' flower spathe lobe growth rate inside the subtending leaf petiole base before emergence. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (MM. DAY^{-1})
0.25
0.20
0.15
0.10
0.05
0.00
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Red color intensity increased rapidly when spathe approached 50% of full development (Figure 12-A), which was 28 days before flower emergence. The color started to appear in the middle portion of the spathe, and then spread upwards and downwards. When the flower bud reached 60% of its emergence length, 50% of the spathe was colored. When the flower bud was going to emerge, 80% of the spathe was colored (Figure 12-A). At this time, the red color could be seen at the swollen petiole base. The lobe portion was the last to develop color. After the flower bud emerged from the petiole base, the lobes remained white for approximately 7 to 10 days.

Spadix Growth And Development Inside The Spathe

The spadix grew slowly inside the tightly furled spathe, and the spadix growth paralleled total flower bud growth (Figure 15-A). The shortest spadix which could be measured was about 0.15 cm when flower bud was 0.7 cm long. The spadix growth in the bud was continuous, with no stop nor decrease in growth rate when both flower bud and spathe reduced theirs (Figure 15-B). It grew from 0.15 cm to 0.42 cm within 35 days with a constant growth rate of 0.07 mm day^{-1}. Then the growth rate doubled, and the spadix length increased to 0.6 cm 28 days before flower emergence. The spadix continued to grow. Fourteen days before flower emergence, it reached 1 cm long, and by the time of flower emergence, it was 1.5 cm long, 50% of the spathe length.

Figure 15-A. *A. andraeanum* 'Kaumana' flower spadix growth inside the spathe before flower emergence. The age of the spadix was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in length. Data are the mean values of flower buds from eight plants. Bars are the variation of the spadix lengths.

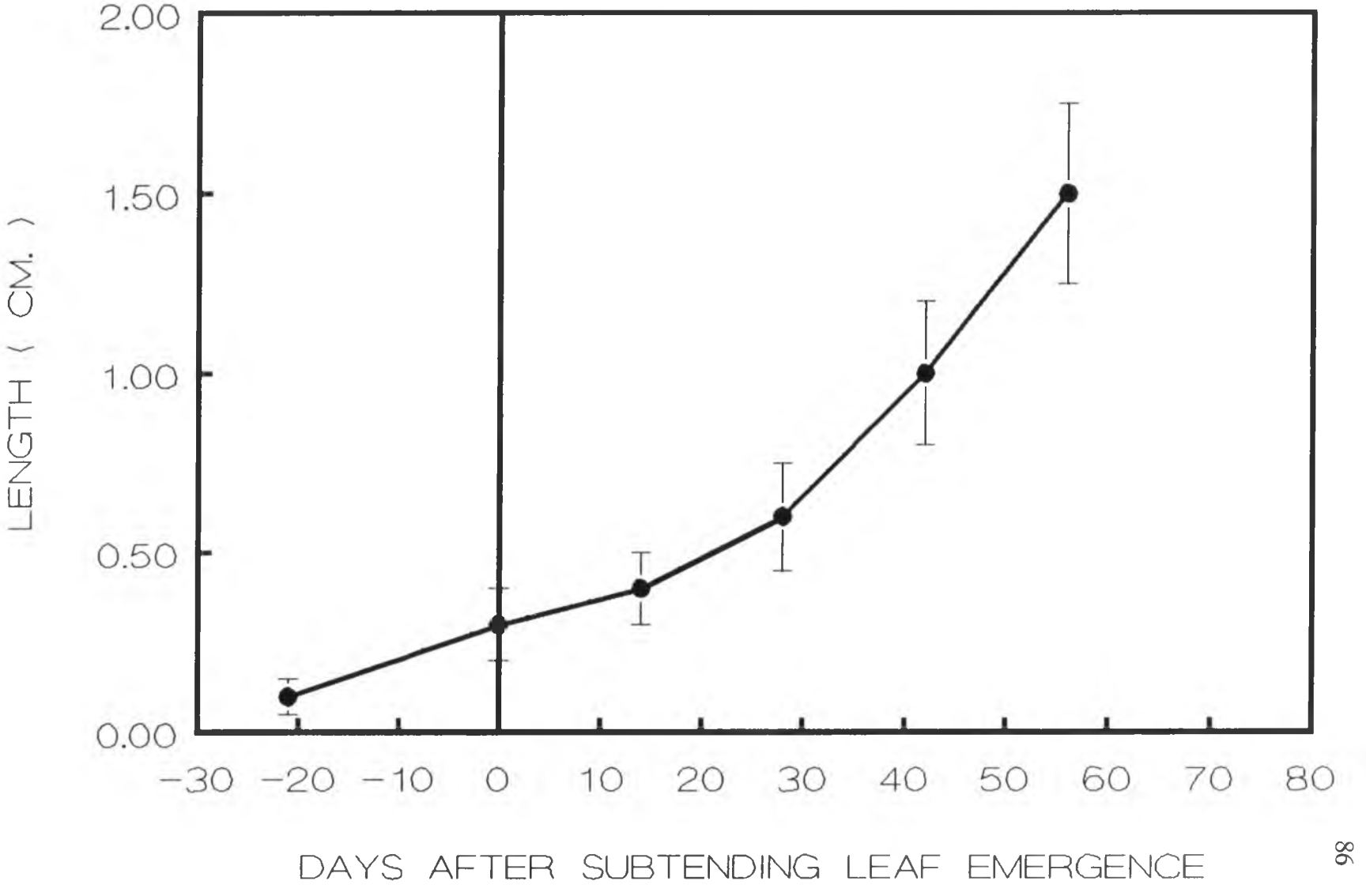
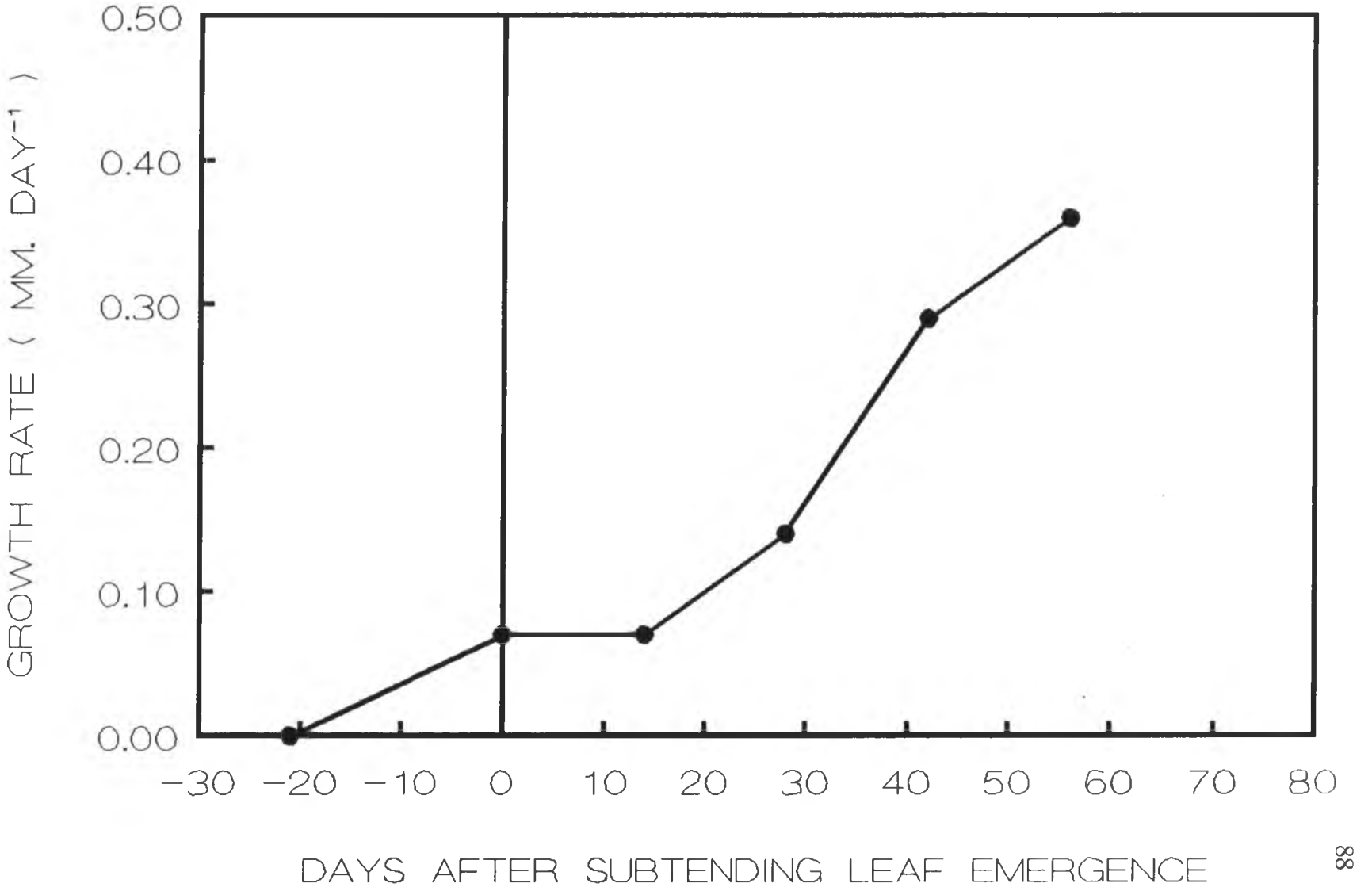

2.00
1.50
1.00
0.50
0.00
LENGTH (CM.)
-30 -20 -10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Figure 15-B. *A. andraeanum* 'Kaumana' flower spadix growth rate inside the flower spathe before flower emergence. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (MM. DAY-1)
0.50
0.40
0.30
0.20
0.10
0.00
-30 -20 -10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Flower Stalk Growth And Development Inside The Petiole

No flower stem growth occurred during the early stage of spadix and spathe development. The length remained less than 0.2 cm for the first 35 days (Figure 16-A). When the flower bud was 1.5 cm long (which was 28 days before flower emergence), the stem growth began to occur (Figure 16-A). The stem elongated rapidly, with a growth rate of 0.21 mm day^{-1} (Figure 16-B) reached 0.5 cm 14 days before flower emergence. During the next 14 days, its growth rate increased to 0.71 mm day^{-1}, and its length reached 1.5 cm when the flower was emerging.

Figure 16-A. *A. andraeanum* 'Kaumana' flower stalk growth inside the subtending leaf petiole base before flower emergence. The age of the stalk was estimated as days after subtending leaf emergence. Day 0 was the time when subtending leaf just emerged from leaf sheath. Before that time, the days were considered negative when the subtending leaf was still in the sheath. Growth was determined as increase in length. Data are the mean values of flower bud stalk from eight plants. Bars are the variation of the stalk lengths.

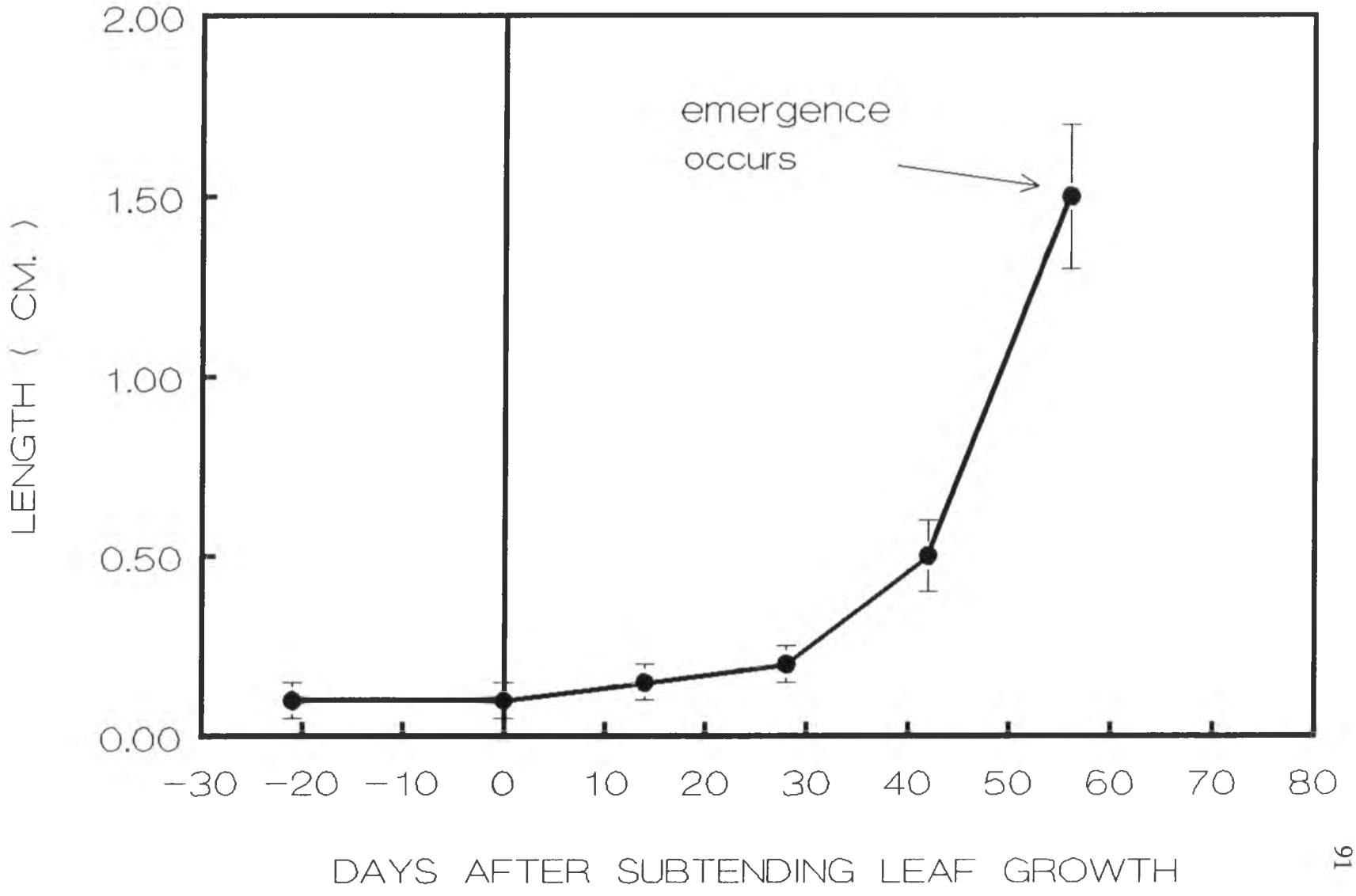
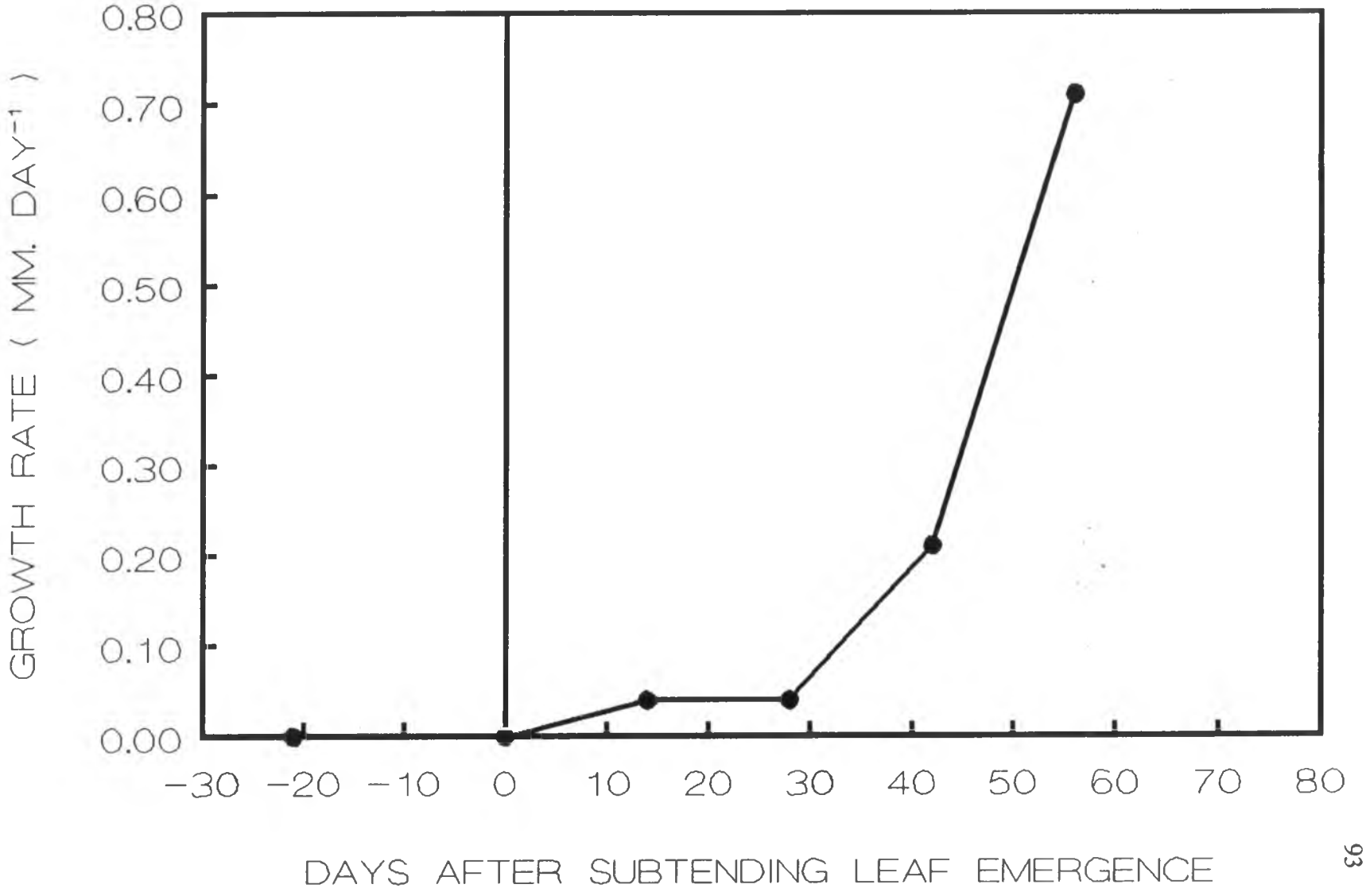

2.00
1.50
1.00
0.50
0.00
LENGTH (CM.)
emergence
occurs
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF GROWTH

Figure 16-B. *A. andraeanum* 'Kaumana' flower stalk growth rate inside the subtending leaf petiole base before flower emergence. Growth rate was determined as change in length divided by change in days.


GROWTH RATE (MM. DAY^{-1})
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
−30 −20 −10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Subtending Leaf Development Effect On Flower Bud Growth Inside The Petiole Base

Relationship Between Subtending Leaf Growth And Flower Bud Growth Inside The Petiole Base

The relationship between subtending leaf growth and flower bud growth inside the petiole base is shown on both Figure 17 and Table 2. When the leaf was still in its sheath, the flower bud had already initiated and had a length of 0.3 to 0.8 cm, 15% of its emergence length (Figure 17). Cell division still occurred at this period. From the day of leaf emergence to day 14 after leaf emergence, the petiole elongated rapidly, 40% to 75% of its emergence length. The growth of the flower bud in the petiole base was suppressed. Twenty-eight days after leaf emergence, as the leaf unfurled, and petiole elongation gradually slowed, flower bud elongation started. After that, the petiole approached its final length, leaf blade became green, and anthocyanin synthesis on flower bud spathe started (Table 2). When the leaf was fully mature and the leaf blade became dark green, the flower bud began emerging.

Figure 17. Subtending leaf petiole growth and the flower bud growth inside the petiole base. Data are the mean values of subtending leaf petioles from eight plants. Bars show variations.

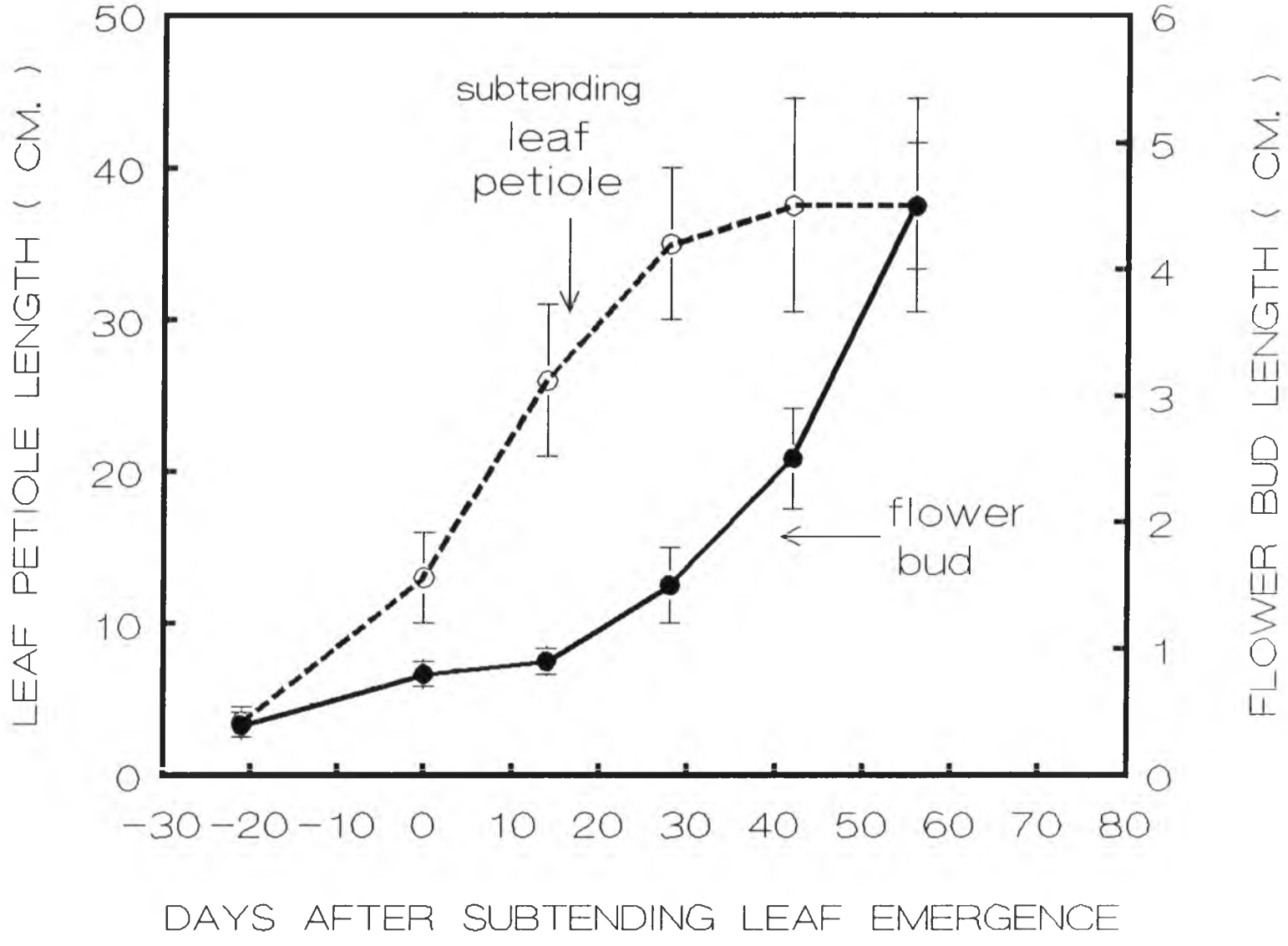

LEAF PETIOLE LENGTH (CM.)
FLOWER BUD LENGTH (CM.)
subtending
leaf
petiole
flower
bud
0
10
20
30
40
50
1
2
3
4
5
6
-30 -20 -10 0 10 20 30 40 50 60 70 80
DAYS AFTER SUBTENDING LEAF EMERGENCE

Table 2. The relationship between subtending leaf growth and flower bud growth inside the subtending leaf petiole base of 'Kaumana'. Six plants were used for each group.

Days after leaf emergence	% final petiole length	Leaf color[a]	Leaf texture	Flower bud length (cm)	Flower bud Characteristics
0	-----	----	----	0.3 to 0.8	cell division
0 to 14	40 to 75	O.B.	crispy	0.8 to 1.0	slow growth
14 to 28	75 to 90	L.G.	soft	1.0 to 1.5	cell elongation
28 to 42	90 to 95	G.	soft	1.5 to 2.5	anthocyanin synthesis
42 to 56	95 to 100	D.G.	hard	2.5 to 4.5	emergence

[a]O.B. Olive brown; L.G. light green; G. green; D.G. dark green. Leaf blade color were determined according to the *R.H.S. Colour Chart* (Royal Hort. Soc. Colour Chart, 1966).

Net Photosynthesis Of Subtending Leaf At Different Ages

Net photosynthesis rate increased as the leaf blade matured. The highest net photosynthesis rate occurred 42 days after leaf emergence when the subtending leaf was mature and dark green (Table 3). The young leaf was olive brown (14 days after leaf emergence) and had a negative net photosynthesis rate (Table 3).

Effect Of Subtending Leaf Removal On Flower Bud Growth Inside Petiole Base

Removal of the subtending leaf at a young stage resulted in earlier emergence of the flower bud (Table 4). The flower emerged 18 days earlier than the control when the subtending leaf was removed when it was still young (approximately 7 to 14 days after leaf emergence). Removal of a light green leaf at day 28 to 35 after leaf emergence also resulted in flower emergence occurring 11 days sooner than the control. Removal of an old subtending leaf (42 to 56 days after leaf emergence) had little effect on flower emergence.

Cultivar Difference

'Marian Seafurth' grew faster and had a flower cycle 30 days shorter than Kaumana (Table 5). Leaf emergence and flower emergence was separated by 30 days for 'Marian Seafurth', whereas 60 days were required for 'Kaumana'.

Table 3. The net photosynthesis rate and stomata aperture of subtending leaf of 'Kaumana' after leaf emergence.

Age (days)	Color[a]	Area (cm^2)	Net Photosynthesis (CO_2 mg m^{-2} s^{-1})	Stomata Resistance (s cm^{-1})
14	O.B.	54 ±29	-0.018 ±0.018	8.3 ±3.0
28	G.	139 ±11	0.038 ±0.012	10.7 ±5.0
42	D.G.	157 ±9	0.105 ±0.009	7.0 ±2.0

[a]O.B. olive brown; G. green; D.G. dark green.

Data are the means of three leaves and ± standard deviation.

Table 4. Effect of subtending leaf removal at various times after subtending leaf emergence on flower emergence for 'Kaumana'. Control was regarded as emerging on day 0 without subtending leaf removal.

Treatments	Flower	At Day 0 of Control	
Cut at days after leaf emergence	Emergence day (days earlier than control)	Stalk length (cm)	Spathe length (cm)
7 to 14	18 ±4[a]	21.5 ±16.9	6.2 ±0.3
28 to 35	11 ±2	12.8 ±7.3	5.5 ±0.5
42 to 50	4 ±4	3.4 ±1.5	4.3 ±0.3
Control	0 ±2	2.8 ±0.4	4.3 ±0.3

[a]Mean ± Standard deviation; n= 6.

Table 5. Comparison of the flower cycle, time between subtending leaf emergence to flower emergence in two cultivars, Kaumana and Marian Seafurth. Flower cycle was determined as the length of time between the emergence of one flower and the emergence of the next flower in the flower-leaf-flower cycle of an individual plant.

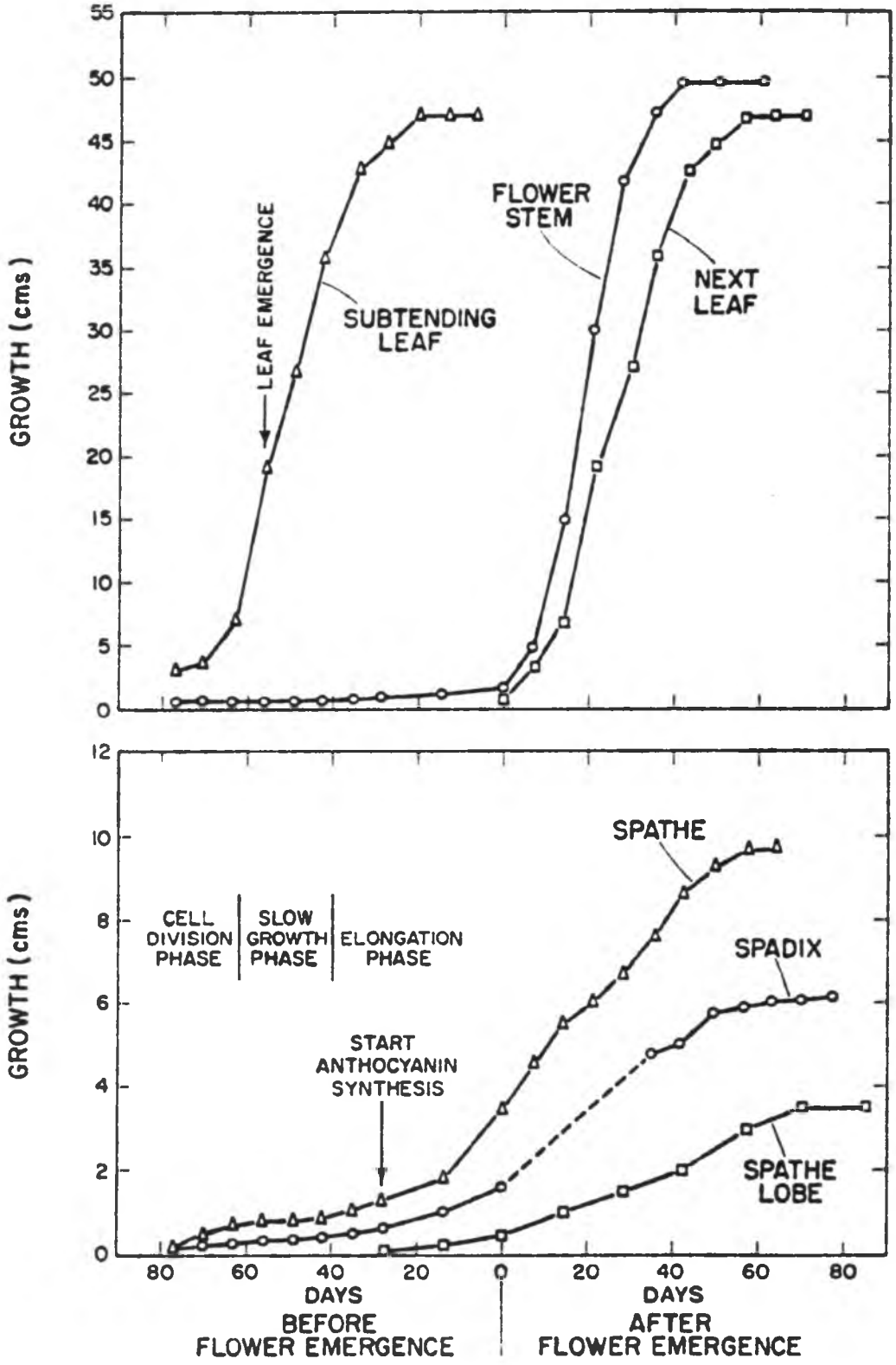
Cultivar	Days needed for one flower cycle	Days from leaf emergence to flower emergence
Kaumana	70 to 80[a]	50 to 60
Marian Seafurth	50 to 60	30 to 40

[a]Values are for 7 plants.

DISCUSSION

The sequence of flower growth after initiation to the full of flower stage was summarized in Figure 18, as well as subtending leaf growth. The whole growth of the flower can be divided into two periods: flower growth before and after emergence. Flower bud growth before emergence could be divided into three phases: cell division phase, slow growth phase, and elongation phase. The cell division phase was the earliest growth phase of flower bud growth after initiation and occurred approximately 80 days before flower emergence. The deformed spathes, wrinkled or curled, might be developed at this stage, probably due to uneven cell division. Following this phase, there was a slow spathe growth phase. During this slow spathe growth phase, the spadix growth rate in the spathe was remained constant. This phase might be the "dormancy" phase termed by Christensen (1971). At this time, the subtending leaf petiole was in the fast elongation period, and the leaf was not fully expanded. The fast growing of subtending leaf might have depleted nutrients and thus slowed flower bud growth. The following elongation phase started about 42 days before flower emergence and continued after emergence. Flower stalk elongation started along with lobes formation in the 28 days before flower emergence. Some dead flower buds had been found occasionally at this phase in this study. The suspected reason for this was that the two stipules protecting the flower bud were too tightly closed, preventing flower bud break-through. Another suspected reason might be that at

Figure 18. Summary of flower stalk and subtending leaf petiole growth after emergence, and flower bud spathe, spadix and lobe growth before emergence.


GROWTH (cms)
55
50
45
40
35
30
25
20
15
10
5
0
LEAF EMERGENCE
SUBTENDING LEAF
FLOWER STEM
NEXT LEAF
GROWTH (cms)
12
10
8
6
4
2
0
CELL DIVISION PHASE
SLOW GROWTH PHASE
ELONGATION PHASE
START ANTHOCYANIN SYNTHESIS
SPATHE
SPADIX
SPATHE LOBE
80
60
40
20
0
20
40
60
80
DAYS BEFORE FLOWER EMERGENCE
DAYS AFTER FLOWER EMERGENCE

this rapid elongation phase, there were not enough nutrients or unfavorable environment conditions caused the flower to die just before its emergence. Spathe anthocyanin synthesis started about 28 days before flower emergence. The lobes did not color until 7 to 10 days after flower emergence.

The anthurium flower bud before emergence was in the subtending leaf petiole base, tightly enclosed by the two stipules. This made the study of flower bud growth before emergence difficult and destructive. Time-lapse surface marking techniques described by Silk (1984) and used for the analysis of anther growth in *Lilium longiflorum* (Gould and Lord, 1988) were impossible with anthurium flower bud growth analysis before they emerge from the petiole base. A developmental index had to be used to study flower bud growth inside the petiole base. The developmental index must be based on recognizable morphological changes with time and non-destructive (Erickson, 1976). Erickson (1948) found that bud length and anther length of *Lilium longiflorum* were highly correlated; therefore the length of an anther could be predicted prior to opening up the bud. Plastonchron index used for *Xanthium* growth studies (Erickson and Michelini, 1957) was not suitable for this anthurium study since the growth pattern of *Xanthium* and *Anthurium* are totally different. The organ that could be used as a developmental index for flower bud growth analysis before emergence might be the subtending leaf. The subtending leaf growth and development such as petiole elongation, leaf blade color and texture changed with time and the measurements of these were not destructive. Therefore,

the flower bud growth inside the petiole base might be predicted from the development stage of the subtending leaves.

Cutting off the subtending leaf at an early development stages did not prevent the flower from emerging, but promoted the emergence (Table 4). This may be because the change of the relationship between source and sink. Young, immature leaves had a negative net photosynthesis rate (Table 3), possibly because the photosynthesis system had not developed, and cells were still heterotrophic (Baker, 1985). Thus, the young leaves were stronger sinks than other parts of the plant, including immature flower buds. Removal of young leaf changed the source and sink relationship, allowing the immature flower bud inside the petiole base to grow. When the subtending leaf became autotrophic (i.e., positive net photosynthesis rate), it also became source for the other sink, flower buds.

Unlike other flowers, the anthurium inflorescence is unique in consisting of flower stalk, spathe and spadix (Higaki, *et al.*, 1984, Paull, *et al.*, 1985). The spathe actually is a modified leaf and the true flowers are born on the spadix (Higaki, *et al.*, 1984). Therefore the growth and development of the spadix might have an influence on spathe development. When the true flowers are initiated, and during the growth and development period, they might produce some substances which trigger anthocyanin synthesis in spathe. After the spadix reached certain length (about 0.5 cm long), the spathe began to color (Figure 18). The bleach problem is also associated with disorder of color development (Bushe *et al.*, 1987). This stage

is in need of more detailed study. Studies of the relationship between the true flower development and spathe anthocyanin synthesis might be worthwhile, but to detach the spadix from the flower bud without killing the bud was impossible.

Anthocyanin coloration on spathe occurred about 30 days before flower emergence when flower bud was longer than 1.5 cm (Figure 11-A). Before this stage, no anthocyanin coloration was observed. The possible reason might be:

(1) In the early growth phase, the phytochrome content was low and had a low response to light;

(2) The flower bud in the early phases was too small, and not sensitive to the light, or the genes which control the flavonoid or anthocyanin synthetase had not been turned on;

(3) The flower bud in the earlier phases was deeply embedded in the petiole base, and the light did not penetrate through the thick stipules to the bud. As the flower bud grew, it became able to detect the light penetrating through the stipules and activate PAL and anthocyanin synthesis.

The environment may have a very important role on anthurium flower initiation and development (Criley, 1985). Temperature affects flower development inside the petiole base and surely affects elongation of the peduncle axis, but this factor has not been studied in anthurium (Criley, 1985). The leaf growth was affected by temperature since leaf emergence occurred one week earlier and had longer petiole length during April to June (24 $\pm 2^{o}$C) period than during January

to April period (20 $\pm 2^{o}$C). The environmental affects on leaf growth would be expected to effect flower bud growth. Reports have shown that flower initiation and development proceed at 18^{o}C and above with an optimum at 20^{o}C and higher (Higaki and Watson, 1973). Leaf-cooling has been reported to improve flower production of anthurium under conditions of high light intensity (Leffring, 1975).

The interval between successive flowers (flower cycle) is not only influenced by a number of environmental factors such as temperature, light, insects, diseases, water, and nutrition, but also affected by genetics (Kamemoto et al., 1986). Days needed for one flower cycle for 'Marian Seafurth' were less than 'Kaumana' grown under the same condition (Table 5). This may due to a shortened period from subtending leaf emergence to flower emergence (Table 5). Flower bud growth and development before emergence for 'Marian Seafurth' were not studied due to not enough plant material.

Flower stalk growth after emergence was sigmoid, which agreed with Kamemoto and Nakasone's work (1963). The spathe growth after emergence was double sigmoid with a constant spadix growth. Spathe lobe was the last to develop, and probably the most sensitive to the bleach problem. But whether it is sensitive before or after emergence is unknown.

The exact cause of bleach problem was not addressed in this study. However, this study does provide basic information about anthurium flower growth and development after flower initiation. The growth and development of the anthurium

flower bud in the subtending leaf petiole base was a continuous process, disruption of the development at any growth stages might cause the developmental problem.

In summary, 28 to 30 days before flower emergence would be the most likely period when growth disruption would be most severe. This was the period when lobe and spadix growth and spathe anthocyanin development occur. Factors that disturbed anthocyanin production at this period may cause bleach problem. A deformed spathe or other similar problems may be the results of uneven cell division, therefore the period 60 to 80 days before flower emergence would be the alternate critical period. Lack of nutrients or severe environmental conditions may cause the flower bud abortion even just before the emergence.

Further studies might be suggested:

(1) Environmental effects: Intensive field study is needed to see how the anthurium plants react under different field conditions; Try to grow anthurium at different locations with different environment conditions and study the growth pattern to see if flower growth and development will react differently;

(2) Cultivar difference: Compare other cultivars with 'Kaumana' to see if different cultivar will have different flower growth pattern and get the growth pattern for the cultivars ;

(3) Light effect on anthocyanin synthesis: Cover petiole base with aluminum foil to determine whether light activates anthocyanin synthesis;

(4) Plant growth regulator effects: Apply growth regulators either on plants or to the growth medium to see if growth regulators modify anthurium flower growth, especially anthocyanin development on the spathe;

(5) Volcanic activities? Apply SO_2 at different concentrations to anthurium plants before and after flower emergence to see if SO_2 will cause the bleach problem and what dosage is critical. Which growth stage is most sensitive to SO_2 needs to be determined.

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